Title
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Publication Date
2019

Peer reviewed|Thesis/dissertation

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by

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A dissertation submitted in partial satisfaction of the

requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor Justin S. Brashares, Chair
Professor Arthur D. Middleton
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Fall 2019

Abstract

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Like much of the global biosphere, wildlife species have experienced rapid declines during the Anthropocene. Wildlife ecologists have responded to these crises by developing a range of technologies, techniques, and large datasets, which together have revolutionized the field, provided novel insights into the movements and behaviors of animals, and identified new risks and impacts to wildlife in a human-dominated world. While these advances have been vitally important, wildlife ecology has been slower to recognize and incorporate humans themselves into its new research domains. The chapters of this dissertation explore methods for better incorporating human behaviors, beliefs, actions, and infrastructure into the theories and approaches in wildlife ecology that have flourished in the last two decades. The research presented here demonstrates the importance of linking human beliefs and behaviors to wildlife ecology both by presenting novel findings and by showing the opportunities missed when narrow approaches are applied to complex socio-ecological problems.

In Chapter 1, I provide a general introduction on the theories underlying this research, contextualize the research questions in light of the loss and recovery of large predators, and describe the research site where I collected much of the data for this dissertation. In Chapter 2, I apply the methods of movement ecology to some of the first fine-scale telemetry data collected on rifle hunters. I draw conclusions about their individual, site-level, and regional-level hunting behaviors and discuss the broad implications of these findings for hunting management. In Chapter 3, I examine livestock-predator conflict using approaches from both ecology and the social sciences. I describe a form of selection bias that is likely widespread but unreported due to the omission of social data from ecological models of conflict, and I offer guidelines for combining and translating ecological and social research on conflict. In Chapter 4, I explore the ecological impacts of one of the most globally widespread human constructions, the fence. I show for the first time the potential extent of fencing at large scales and discuss the wide variety of ecological effects of fences for both humans and ecosystems. I further highlight biases and gaps in fence research that have thus far limited a complete understanding of the environmental effects of these features. In Chapter 5, I conclude by making recommendations regarding how research might better incorporate human perceptions, decisions, and actions into ecology.

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Acknowledgements

What you read in this dissertation is a version, a very polished and defensible one, of a series of ideas, discussions, trials, failures, moments of joy and sorrow, moments of turbulence and clarity, all working toward bigger ideas and new conversations. Acknowledgements can't do justice to the contributions and collaborations of the many I'll mention here and many more I won't. They have all been authors in their own way.

First, I thank my advisor Justin Brashares, a tremendous source of personal and professional support, a great mentor and collaborator, and an inspiring scientist to learn from and work alongside. I leave this degree more capable, confident, and compassionate thanks to his advising, and I'm grateful to call him a colleague and a friend.

The members of my dissertation committee have transformed the way I think about and conduct research. I will always strive for Mary Power's clever and creative thinking, and I remain inspired by her endless wonder at the patterns and processes of the natural world. Arthur Middleton's ability to see through disciplinary and methodological boundaries and explore the meaningful questions at the heart of things is how I hope to approach research.

I cannot overstate my thanks to the members of my lab group for their wisdom, insight, support, humor, and friendship, and I am proud of and grateful for all we've done together. Katie Fiorella, Tristan Nunez, Katy Seto, Cheryl Hojnowski, Ryan Marsh, Mario Klip, Dave Kurz, Phoebe Parker-Shames, Kendall Calhoun, Amy Van Scoyoc, Millie Chapman, Lindsey Rich, Jessie Moravek, Mitch Serota, and Guadalupe Verta, you made it matter, and you made it fun. Briana Abrahms, thanks in particular for making me feel welcome from day one, and, let's not forget, introducing me to Wilson. Lauren Withey, working through our weekly goals, or often not working through them, was just an excuse to spend more time with a good friend. Eric Dougherty, when you track down Potsy, let's go back into the woods together. And Kaitlyn Gaynor, I don't think I could have done it without you, you're a remarkable thinker, an indefatigable colleague, and a great companion behind the desk and on the road. I look forward to our next chapter in Santa Barbara.

My qualifying exam committee provided one of the most fun and informative semesters at Berkeley, and I thank Tony Barnosky for his thoughtfulness, Ian Wang for his careful attention to detail and theory, and Adina Merenlender for her diligence and support as my committee chair. I offer a special thanks to Bob Hass, who has been a mentor, friend, and a wellspring of curiosity and wonder for many years. His sponsorship of my ecopoetry class made one of the most important facets of my time at Berkeley possible. I also thank Bree Rosenblum for her wise mentorship, and for training me to be a caring and dedicated mentor in turn. A special thanks goes to Doug McCauley and Hillary Young, without whose mentorship and trust I would have never had so many opportunities, from my first expeditions in the field to graduate school and more.

I have worked with terrific collaborators throughout my time at Berkeley, several of whom are mentioned above, and I give further thanks to them and to Wenjing Xu whose dedication to fences and to goodness helped make me a better scholar, to Christine Wilkinson who reminded me that you could accomplish a lot without taking it quite so seriously, to Owen Bidder and Justine Smith who somehow made statistics fun, and to Jennie Miller, who has been a constant source of support. A special thanks goes to staff members at the Hopland Research and Extension Center, including Tom Seward, Zane Kagley, Amber Shrum, Brooke Gamble, and

Shane Feirer, without whom much of this research could not have happened, and all of whom offered another wonderful reason to go into the field. Alison Smith in particular is a role model in all walks of life, Troy McWilliams would be a role model were he not a real life superhero, Hannah Bird never made a place feel more like home, Jim Lewers helped change the way I think about the working landscape, John Bailey was tireless in his support, and Kim Rodrigues's dedication to coexistence inspired several questions in this work. Field staff worked admirably on our behalf, and I'm grateful for the contributions of Jessie Roughgarden, Lara Brenner, and especially Janelle Dorcy, who happily and deservingly has joined our ranks in graduate school. Bryan Bach and Ashling Quigley worked relentlessly behind the scenes, never complained, and were always a pleasure to meet in or out of the office.

Berkeley undergraduates also played a crucial role in this research, and I'm grateful for the many who toiled over camera trap images, shepherd's journals, and spreadsheets: Yana Slabakov, Muhib Haidari, Sky Korber, Alex Wood, Ben Pridonoff, Soledad Soto, Mikaila Baskin, Mindy Liou, Karen Chow, Erin Griffin, Emily Carter, Jessica Maccaro, Catherine Jung, Jennie Green, Roxanne Gardner, Megan Banke, and Alex Goetz. I'll offer a special thanks to Tyler Cino, whose enthusiasm and hard work were essential to some of the foundations of this research, and to Sami Kreling, Lara Volski, Vicki Guan, and Margot Barker, whose thesis research kept me inspired and engaged.

In the proud tradition of Soorim Song, there are important animals to thank, including Felipe, at different times my brother, father, and son; Luke, who made me love dogs; Circle and Lila, who played the best game of mousetrap I've ever seen; guardian dogs Jasmine, Otie, Bebo, Nate, Red, and Rocky (rest in peace), who are the hardest workers of us all. Pip gets thanked too, and, last but not least, even friendly Nat, who won me over in the end.

Finally, friends and family away from the academy were constant sources of support and joy, and there are too many to name who have made life worth living. Special thanks to Peter for many roofs over my head and years of brotherhood, to Adrian, another brother in the arts and co-sponsor of the loudest and best gradfest ESPM will have ever had, Amanda and Jamie, whose humor and support always give me another way of looking at things, and to Clare, my oldest friend, who helped get me into this mess and helped get me out of it too. Moon, this last year I owe to you, you've somehow made a year full of the hardest things in life into one of the best years in life. Finally, I thank my parents, Michael and Robbin McInturff, for challenging me and supporting me in turn, making me believe this was possible, and showing me through example what good deeds and what remarkable lives can come of it. I would not be here without you.

Chapter 1. Introduction

CHANGING ECOSYSTEMS, TECHNOLOGIES, AND PERSPECTIVES

As the 21st century dawned, scientists delineated a novel geological epoch, the Anthropocene, defined by the globally recognizable, long-term impacts of human activities (Steffen et al. 2007). In the past two decades of this era, wildlife ecologists have identified particularly rapid declines in large terrestrial species due to habitat loss and fragmentation, overexploitation, and an expanding human footprint that continues to place humans and wildlife into increasing conflict (Brashares et al. 2014; Ripple et al. 2015; Wolf & Ripple 2017). Such drastic changes demand novel approaches, and the last two decades have also witnessed astonishing advances in the field of wildlife ecology. During this span, multiple technological revolutions have reshaped the field: geographic information systems have matured (Gewin 2004; Rundel et al. 2009), telemetry data to track animals has become widespread (Wilmers et al. 2015), and computational power has increased to support fine-scale and global analyses that were impossible in the recent past (Hampton et al. 2013). These technologies have simultaneously inspired hope for opportunities to mitigate threats to wildlife and shed light on new risks for wildlife on a changing planet.

Alongside technological advances in wildlife ecology, there is a growing recognition that human beliefs and behaviors must be taken seriously as both causes and consequences of ecological change (McDonnell & Pickett 2012). Traditionally, ecology focused on systems with minimal human disturbance where "rules" of nature might be discovered (Martin et al. 2012), but the scale and pace of global change in the Anthropocene have increasingly urged ecologists to consider humans as active participants in natural processes (Miller & Hobbs 2002). Humans have been classified, for example, as a global "super predator" due to their competitive dominance over apex predators (Darimont et al. 2015), and human activities have been shown to cause a wide range of species to alter fundamentally their habitats and behaviors (Suraci et al. 2019, Gaynor et al. 2018).

As important as this human turn in ecology has been, gaps remain, and questions about human relationships with the environment still have potential to make critical headway in understanding and mitigating global wildlife declines. While important discoveries about the ecological agency of humans have been made at the broadest scales, the consequences of smaller-scale human movements and behaviors remain a mystery. Even in spite of the high cost of wildlife telemetry, we likely know more about the ecological consequences of the movement and behavior of species like pumas and cheetahs than we do humans (Wilson et al. 2013; Williams et al. 2014). Applying the groundbreaking methods and tools that have reshaped wildlife ecology to humans has untapped potential in revealing human movements and behaviors with profound ecological consequences.

Research has also shown an important role of including stories and beliefs into questions about the environment, as these ultimately inform decisions and actions that can materially impact ecosystems (Cronon 1992; Bruskotter & Wilson 2014). The field of human-wildlife conflict in particular benefits from socio-ecological approaches, in which human beliefs and actions are framed as reciprocally linked with the environments in which they are embedded (Dickman 2010). Interdisciplinary research that incorporates methods and findings of social science has helped inform approaches to human-wildlife conflict and other drivers of wildlife decline that have been equitable and long-lasting (Woodroffe et al. 2005; Manfredo 2008;

Baruch-Mordo et al. 2009). Human lives and livelihoods are also at stake under conditions of environmental decline, and incorporating the ecological and social dimensions of human activities into ecology helps mitigate connected consequences for people and wildlife (Brashares 2004; Brashares et al. 2014).

In this dissertation, I combine novel technologies in wildlife ecology with novel considerations of human behaviors and beliefs as constituents of the environment. In Chapter 2, I present an analysis of the movement and behavior of humans during one of the most ancient forms of environmental interactions, the hunting of wild game. In Chapter 3, I discuss a suite of approaches for incorporating human perceptions into ecological models of human-wildlife conflict. In Chapter 4, I examine the interconnected ecological effects on people and wildlife of one of the planet's most ubiquitous but understudied features, the fence.

PREDATOR RECOVERIES AND COEXISTENCE

The questions of this dissertation are framed amid widespread predator declines and rare recoveries. Of the many kinds of wildlife declines throughout the world, the declines among large predators are among the direst (Ripple et al. 2014, Wolf & Ripple 2017). The loss of any species may cause concern, but losses of large predators in particular have far-reaching consequences, as their effects cascade down trophic levels, altering whole ecosystems (Estes et al. 2011). As a result, community ecologists and conservation biologists alike have broadcast the need for large predator conservation.

In some areas of the world, predators are in fact making recoveries, making these locales exciting laboratories for studying conflict and coexistence between humans and wildlife. In the western United States, after several centuries of systematic predator extirpations (Reynolds & Tapper 1996), an ongoing series of economic, legal, and cultural changes have supported large predator recoveries in the past few decades (Berger 2006; Bergstrom 2017). California in particular has passed several laws at the state level that further support the recovery of predators by restricting the methods and circumstances in which predators can be hunted or killed.

In sites like these where predator recoveries are successful, human relationships with these animals and human activities in the environment more broadly are likely to change. Where human populations are rapidly growing, especially at the wildland-urban interface, the stage is set for increased conflicts with recovering predators (Marshall et al. 2016). These recovering predators may pose a threat to people's lives and livelihoods (Graham et al. 2005; Muhly & Musiani 2009; Widman & Elofsson 2018), and retaliatory killings of predators may threaten the long-term success of recoveries (Treves & Karanth 2003). Predators may also compete with humans for similar food sources, thus altering patterns of human hunting and behavior (Marshall et al. 2016). In response to predators, humans may further expand or fortify infrastructure, such as fences, to mitigate conflicts (Stone et al. 2017). The high stakes of predator recoveries for the predators themselves, the ecosystems in which they occur, and even for humans has prompted growing interest in "coexistence" between humans and predators (Dickman 2010).

The chapters in this dissertation work to better incorporate human behaviors, beliefs, and infrastructure into the growing body of science on human-wildlife coexistence. The second chapter improves our understanding of the ecological mechanics of humans as hunters. This research will help understand how humans may compete with wild predators for prey as respective populations grow and how the differential lethal and non-lethal consequences of

human and wild predators may impact prey species and their ecosystems. The third chapter offers new methods for bringing human perceptions and experiences regarding conflict with predators into dialogue with ecological models of conflict. This chapter provides important tools and guidance for future practitioners of predation risk modeling, an increasingly popular non-lethal tool for mitigating livestock-predator conflict. The fourth chapter examines one of the primary infrastructural tools, the fence, deployed to facilitate coexistence between humans and predators. This chapter points out the glaring research gaps on the often-unanticipated effects of fences on all scales of ecology.

STUDY SITE

Much of the primary data collection in this dissertation was conducted at the University of California's Hopland Research and Extension Center (Hopland) in Mendocino County, California. While Hopland serves as an ecological research station, the unique activities taking place at the site make it a revealing microcosm in which to ask the questions covered in these chapters. Hopland has a rare mixture of research histories, serving as a nationally recognized hub for research programs on both wildlife and domestic livestock. Recently, researchers and staff alike have observed recoveries of multiple large predators at the site. Hopland is poised at the interface of rural agricultural production and wildlands, and findings regarding human-predator conflict and co-existence at this site thus have broad applicability.

Another unique characteristic of Hopland is that every year, the site hosts a public hunt for Columbian black-tailed deer (*Odocoileus hemionus columbianus*). The rare combination of a hunting ground on a research station supported the unprecedented data collection in Chapter 2 on the movement and behavior of hunters at the site, who likely typify public lands hunters in California and beyond. Findings here also reflect human hunter behaviors in the context of recovering predators.

As a livestock production center, Hopland has supported research into non-lethal tools to mitigate conflict between recovering predators and sheep. Additionally, livestock producers on the site keep extraordinarily detailed records on conflict occurrences, and this data underpinned the research conducted in Chapter 3. Livestock producers locally and across the state turn to Hopland for its findings on non-lethal tools for addressing livestock predation, meaning that research conducted here has a ready conduit to management and application.

Finally, Hopland is latticed with fences of many types, heights, and conditions. Questions arising around observations of wildlife movements and ecological patterns radiating from these fencelines were a crucible from which the broader questions explored in Chapter 4 emerged.

OVERVIEW OF DISSERTATION

In Chapter 2, "The movement ecology of the human 'super predator' on public lands in California," I examine one of the most ancient human environmental behaviors, the hunting of large herbivores. The combination of GPS telemetry and the analytical techniques of movement ecology have revolutionized our understanding of predator-prey dynamics among wildlife species. Movement data have revealed that the mode and pattern of hunting taken up by wild predators has profound consequences for prey survival. Just as importantly, research has unveiled the vital importance of non-lethal aspects of hunting. By their presence, behavior, and

movement, predators can influence prey decisions, movements, and habitat selection to such a degree that these non-lethal effects may have more pronounced consequences than lethal ones. As rapidly as our understanding of wild predators has grown, the movements and behaviors of the human "super predator" have largely been ignored. In this chapter, I apply the techniques of movement ecology to data from GPS-tracked rifle hunters of black-tailed deer on a public land in northern California. The unprecedented granularity and coverage of these data supports analysis of individual hunter behaviors, site-level trends with lethal and non-lethal implications, and a regional projection with broader implications for the connection between human infrastructure – namely roads – and hunter behavior.

While Chapter 2 examines humans using the tools of wildlife ecology, Chapter 3, "Patterns of coyote predation on sheep in California: A socio-ecological approach to mapping risk of livestock-predator conflict," considers how techniques drawn from social science might be paired with ecological models to improve understandings of human wildlife conflict. This chapter takes advantage of a unique dataset detailing the location and condition of livestock-predator conflict events in which domestic sheep were killed by coyotes. These data supported the development of an environmentally-driven predation risk model, an increasingly popular ecological tool for predicting and mitigating conflict. While such models have been used in the past to "correct" producer perceptions of conflict risk, I use participatory mapping and a questionnaire of producer perceptions to complement this environmentally-driven predation risk model. In doing so, I provide evidence for an overlooked source of selection bias that is likely widespread in ecological models of livestock predation, and I further suggest strategies for better translating between social and ecological models of conflict.

Chapters 2 and 3 directly deal with the question of how human behaviors and beliefs manifest in both the environment and in ecological research. In Chapter 4, "Holes in the fence: The ecological effects of fencing are widespread but poorly understood" I examine one of the most ubiquitous physical manifestations of human beliefs about the environment, the fence. Fences encircle the planet and for millennia have played a central role in defining the human relationship with the environment. Nevertheless, research on fences has been idiosyncratic, typically focusing on a single species or aim, and fences have been ignored in global estimations of human impacts. In this chapter I survey the global ecological effects of fences. In a systematic literature review I characterize the impacts of fences at every scale of ecological analysis, and show their effectiveness at reorganizing ecological winners and losers in the systems where they occur. I present one of the first large-scale maps of fences to demonstrate their ubiquity and their simultaneous omission from well-known measures of the human footprint. Finally, I provide a series of frameworks to guide future research and highlight the biases and gaps that have limited a productive "fence ecology."

In Chapter 5, "Concluding remarks," I consider the themes that emerge from this diverse body of research, and I discuss further the roles that ecologists may play in understanding and dampening the rapid environmental changes of the Anthropocene. I conclude by discussing the importance of stories to ecology and the future of human-wildlife coexistence.

Chapter 2. The movement ecology of the human "super predator" on public lands in California

ABSTRACT

Humans have become a global "super predator," yet human hunting behaviors have gone almost entirely unexamined. Simultaneous advances in the theory of movement ecology and availability of GPS telemetry have supported a revolution in our understanding of the movement and behavior of wild prey, but these techniques and technologies have rarely been applied to human hunters. While the catastrophic lethal effects and management importance of human hunting are well documented at broad scales, the absence of fine-scale research on hunting behavior means that patterns and mechanisms of effects of human hunting on wildlife are not well understood. Here, we took advantage of a public hunt on a University research station to deploy 302 GPS collars taking 10-second fixes on hunters of black-tailed deer in California. We used first passage time to segment individual hunting behaviors, Brownian bridge movement models to predict the spatial patterning of hunting pressure, and linear regression to link hunting pressure to environmental covariates and make projections at a regional scale. Across all three scales – individual, site, and regional – roads stood out as an important predictor of hunting pressure. Our research suggests that the links between roads and the lethal and non-lethal effects of hunting on game species deserve further scrutiny from scientists and managers alike.

INTRODUCTION

From the Pleistocene to the present, human hunting of wildlife has altered ecosystems and driven species declines throughout the world (Barnosky 2004; Darimont et al. 2009; Ripple et al. 2014; 2015). Humans have become so competitively dominant as predators that some have argued they occupy a novel evolutionary position as a global "super predator" (Darimont et al. 2015). Simultaneously, hunting also provides an essential tool for the management of wildlife populations, especially for game species like ungulates. Where large carnivores have been extirpated from ecosystems, overabundance may have direct and cascading impacts that can entirely reshape ecosystems when hunting by humans does not keep pace with population growth (Côté et al. 2004; Nugent et al. 2011; McShea 2012; Williams et al. 2013). Hunting thus represents one of the most influential interactions humans have with wildlife, and the precision with which it is managed has far-reaching consequences for game species and their ecosystems.

While hunting is widely recognized for its roles as both a conservation tool and a driver of decline, we have a surprisingly poor understanding of the ecological mechanics of hunting itself. The science and management of hunting has historically focused on its broad-scale numerical effects on prey species, and there is almost no research on the fine-scale movement and behavior of hunters (Lebel et al. 2012; Kuijper et al. 2013a; Le Saout & Padié 2014). However, a recent and growing body of literature in wildlife ecology makes clear that fine-scale movements and behaviors of predators have enormous and measurable effects on ecosystems (Lima 2002; Mitchell & Lima 2002; Creel et al. 2013b; Wilson et al. 2014; Wilmers et al. 2015). Research on predator movements has provided insights into the spatial variation of the lethal effects of hunting (Wilson et al. 2013; Smith et al. 2015; Isbell et al. 2018), but it has also helped unlock novel questions into a broad-array of non-lethal consequences of predators (Peacor &

Werner 2001; Eriksen et al. 2011; Kuijper et al. 2013b; LaManna & Martin 2016). Analyses of fine-scale predator movements have shown that individual prey behaviors and fitness can readily be altered by the risk of predation, but so too can larger scale patterns of habitat and resource selection (Schmitz et al. 2004; Suraci et al. 2019). Through their movements and hunting modes, predators can even create "landscapes of fear" that may be as or more important as direct mortality at a range of scales and for a range of ecological phenomena (Gaynor et al. 2019). Recent studies have demonstrated the indirect, non-lethal effects of hunting using GPS collars on game species (Karns et al. 2012; Bonnot et al. 2013; Le Saout & Padié 2014; Stillfried et al. 2015), but little research has examined human hunters using these methods.

Given the importance of understanding the fine-scale movement and behavior of predators, the dearth of research that has examined the human "super predator" in this light is glaring. As ecology moves forward into the "golden age of bio-logging" (Wilmers et al. 2015), there is arguably a more nuanced understanding of the hunting mechanics of species like pumas and cheetahs than of humans (Wilson et al. 2013; Williams et al. 2014; Wilson et al. 2014; Wang 2015). A range of movement ecology approaches and commercially available GPS technologies have the potential to rapidly overcome this knowledge gap. As with wild predators, mapping GPS clusters from hunters can precisely identify kill site locations and help establish patterns of lethality for game species (McInturff, unpublished data). Just as importantly, GPS telemetry can reveal patterns in hunter movement and behavior that have non-lethal consequences for game species and non-game species alike. For example, studies have shown that game species dramatically alter behavioral responses to hunters depending on whether they are in or out of cars (Stankowich 2008). Movement ecology metrics can distinguish area-restricted search behavior, in which hunters are actively stalking deer on foot, allowing for the identification of areas where non-lethal effects are likely to be higher (Abrahms et al. 2017). More generally, distinguishing behavioral states of hunter can further refine our understanding of individual and group decision-making by hunters and their consequences for prey (Papworth et al. 2012; Rosetti et al. 2015). Applying utilization distributions like kernel densities or Brownian bridge models may identify effect zones of hunting pressure at broader scales. At even larger, management-relevant scales, an understanding of hunter movement patterns allows for linkages between behavior and environmental characteristics that support predictions for conservation and management. These methods have made important contributions in related fields, such as the management of recreationists (Beeco & Hallo 2014) and fisheries (O'Farrell et al. 2019), but have had limited application in terrestrial hunting (Stedman et al. 2004; Lebel et al. 2012; Jones et al. 2017).

In this study, we deployed small, affordable GPS tracking units to rifle hunters of black-tailed deer (*Odocoileus hemionus columbianus*; hereafter "deer") in California from 2015 to 2017. We took advantage of a public hunt on a research station to track every hunter on the site at a 10-second fix interval, representing unprecedented coverage of hunters and granularity of data. We used hunter GPS data to test hypotheses about hunter movement and behavior at multiple scales. At the smallest scale, we predicted that individual hunters would spend most of their time within a short distance of roads (Stedman et al. 2004; Lebel et al. 2012; Jones et al. 2017) and would select for grassland habitats that were flat or offered long views. We predicted hunters would avoid site boundaries adjacent to non-huntable lands (Adkins & Irby 1994), but that they would preferentially hunt near the neighboring BLM protected land, following trends in other systems (Tolon et al. 2012). We predicted that hunter behavior would show a clear

distinction between driving and area-restricted searching on foot, and that patterns of behavior and hunting pressure would differ across these two behavioral states. At the scale of the study site, we examined whether cumulative individual hunter behaviors would create recognizable patterns that would reflect both the lethal and non-lethal effects of hunters on the landscape. We expected cumulative hunter movements to exert hunting pressure at highest levels where road densities are high, terrain ruggedness is low, and vegetation density is low (Bonnot et al. 2013). We expected visibility and vegetation to play a greater role in hunting pressure during area-restricted searching on foot. We predicted that, taken as a group, hunter movement and behavior would be consistent with the location of contemporary and historical kills sites, showing strong overlap between spatial patterns of lethal and non-lethal effects. Finally, because research rarely links fine-scale movement to harvest management (O'Farrell et al. 2019), we asked whether inference from these fine-scale data could inform regional patterns. Fine-scale findings can have the greatest impact if they are scalable to large management units most relevant to practitioners. At this regional scale, we predicted that large spatial refugia from hunting pressure would be available in the region's many roadless areas, while the lethal and non-lethal effects associated with hunting pressure would peak around publicly available road networks.

METHODS

Study area

We conducted primary data collection at the 2,168-hectare Hopland Research and Extension Center (HREC) in Mendocino County, California (Latitude: 39.002, Longitude: -123.084; Figure 1). HREC is a research facility operated by the University of California near the geographic center of California's Zone A (North Unit 160) hunting zone. The site features habitat types characteristic of this hunting zone and of the California Coast Range mountains more broadly, including grassland, oak woodland, and chaparral. The site is served by a network of dirt roads, and has a series of fences constructed for a flock of 600 sheep managed by the research center. Researchers have studied black-tailed deer (*Odocoileus hemionus columbianus*) at this site, including recording kill sites by hunters, for several decades, making it an ideal location for further research on the species. Several predators of black-tailed deer have also made recoveries at this site, including black bears (*Ursus americanus*), mountain lions (*Puma concolor*), and coyotes (*Canis latrans*).

The site is bordered to the north by a large (25,000 hectare) and remote Bureau of Land Management (BLM) property that provides undeveloped connectivity to the Mendocino National Forest. To the south, the site abuts agricultural and residential development along the Highway 101 corridor. None of these neighboring properties share the same hunting management practices as HREC.

During the first three weekends (Saturday and Sunday) of the California Zone A hunting season in August, the site hosts a public hunt. 20 hunters per day are selected by lottery from a pool of applicants, and a maximum of 120 hunters per year hunt at the site. Two small pastures and the area surrounding site headquarters are off limits to hunters (Figure 1).

Data collection

From 2015-2017, we invited hunters at the study site to participate in our study. We had a 100% rate of participation (n = 302). During a pre-dawn orientation to the site, we introduced

participating hunters to our research project, made clear that they would remain anonymous as participants in this research, and showed them the GPS tracking units they would be carrying. We asked hunters to note the time of any shots taken, whether shots were successful, and the time during which they conducted field dressing. We also asked hunters to keep track of the number of bucks, does, and fawns they observed during their hunt.

We provided each hunter with a small GPS unit (i-gotU GT-600, Supplementary Figure 1) that was programmed to take a GPS fix every 5 seconds from 5am to 10pm. Hunting is legal only during daylight hours, from approximately 6am to 9pm during this time of year at the study site. We asked hunters to keep the GPS unit in a pocket that would remain on their person, even when they were moving on foot.

Data cleaning and subsampling

After collection, we removed all GPS points that occurred off the study site or fell within the hunting prohibited zones. We also removed any GPS points collected before dawn or after sunset. We subsampled data to a 10-second fix rate to speed computation time and account for missed fixes from the original 5-second data collected.

Hunter input

While we did not formally interview hunters, our discussions with them helped refine our characterization of their movement behavior. In discussions with hunters at the study site, we gathered that hunters were economical with their time spent on the site, spending little to no time on activities other than active hunting. This is unsurprising, given that the site is a highly desirable hunting location, and hunters selected by lottery are limited to a single day at the site. As a result, we assumed that time spent in the huntable zone was active hunting time. Many hunters chose to eat lunch at the site's headquarters within the hunting-prohibited zone, but GPS points from this area were removed from the analysis, as described above. Hunters averred that their time spent in the huntable zone was spent either driving while searching for deer or actively stalking or pursuing animals on foot. Several hunters recounted that they continued actively searching for legal bucks even while pursuing an animal that they had already killed or wounded.

Hunter space use

For individual hunters and for the group of hunters at large, we calculated several metrics of space use. We examined distance from roads, boundaries, and neighboring protected areas. We calculated these distances at variable radii and compared them to the corresponding portion of the study site that these radii occupied.

Behavioral segmentation

We explored multiple approaches for behavioral segmentation of hunter GPS locations in the huntable portion of the study site. Previous research in movement ecology has used step lengths and turn angles to determine when animals are foraging. Foraging is often typified by shorter step lengths and more sinuous turn angles, and cut-offs can be developed to identify these behaviors based on statistical examination of these characteristics (Gurarie et al. 2009). However, when step lengths are very small, GPS error may be greater than cutoff lengths and result in inaccurate classifications (Frair et al. 2010).

An alternative approach to step-length and turn-angle segmentation of behaviors is to use first passage time (FPT). First passage time (FPT) measures the length of time an animal spends within a given radius and, since its introduction to the analysis of animal movement, has become a favored approach for identifying area-restricted search behavior, which is characteristic of hunters stalking prey on foot (Fauchald & Tveraa 2003; Abrahms et al. 2017). We used FPT to distinguish between time spent searching or exploring by car from time spent actively stalking animals. We first calculated the FPTs for all hunter data across a range of radii. We then plotted the variance in FPT against these radii to identify a characteristic scale of area-restricted searches, such that variance in FPT is maximized. We conducted analyses in the adehabitatLT package in R (R Core Team 2018), and identified a local variance maximum at a radius of 40 meters, which we used in our calculations (Supplementary Figure 2). We then identified a characteristic FPT for this radius. Data displayed a bimodal distribution, with 900 seconds (15 minutes) providing an approximate cutoff between behavior types using this approach. We tested a range of radii from 10 to 80 meters and found that this bimodal distribution persisted regardless of radius, with 900 seconds providing an appropriate cutoff. We partitioned data between area-restricted search (ARS) behavior and exploratory driving (ED) using these parameters.

Estimating hunting pressure

To estimate the cumulative lethal and non-lethal patterns of hunter space use, we used a Brownian bridge movement model (BBMM) to estimate hunting pressure using the package adehabitatHR in R (Horne et al. 2007). We made two separate calculations, first using the entire data set and then using only the area-restricted search data identified by first passage time. BBMMs have been widely used to estimate animal home ranges from telemetry data (Abrahms et al. 2017). BBMMs account for serial autocorrelation in telemetry data, which is a particularly important issue given the high fix rates of GPS locations of hunters in this study. They also incorporate the range of potential movements between fixes, making them a more robust and ecologically informed estimator than kernel density estimators.

BBMMs are defined by two parameters, which are typically derived from movement and telemetry characteristics when defining animal home ranges (Horne et al. 2007). Because we were not attempting to define a home range, but rather a characteristic level of pressure surrounding hunter locations, we set the first parameter manually to 250 meters. This was a reported approximate upper distance for successful detection and stalking of deer at the study site and an upper limit of deer detection distances in the literature (McNay et al. 1994; Koenen et al. 2002; LaRue et al. 2007). We calculated a BBMM for each individual hunter and summed these into a single raster layer. We repeated our analysis at a range of parameter values from 200 to 300 meters, but found little difference in the patterns of the produced distributions. We conducted this process for all our data (from here forward “full model”), and for a subset of area-restricted search data parsed out by FPT (from here “ARS model”).

Finally, to test whether these models of hunting pressure based on movement corresponded to the lethal effects of hunting, we first examined the overlap of kill sites at the study site with areas >1 standard deviation above mean hunting pressure according to both the full model and ARS model. We located these kill sites by identifying GPS clusters in the data then finding the sites in the field. We also conducted a linear regression of both hunting pressure models against a previous model of hunting risk conducted on site. This previous risk model

used a historical database of kill sites dating back several decades to estimate mortality risk for deer at the site (Gaynor 2019). We calculated R^2 values for these two regressions.

Environmental covariates of hunting pressure

We conducted linear regressions to estimate environmental covariates of hunting pressure for both the full model and ARS model. For each of these two models, we first extracted environmental covariates for each raster cell from available environmental data or derived from primary data collection (Supplementary Table 1). Because we wanted to examine a large number of environmental variables, we used a hypothesis-driven approach to narrow these variables down. We first grouped variables into categories of topography, human presence and infrastructure, and habitat. We used model selection in a maximum likelihood framework to determine top regression models in each category (models within 2 delta AIC of the top regression model). We then combined the variables retained in these top regression models into a single candidate model, again applying a maximum likelihood approach to select a final regression model, which gave estimates for the environmental covariates of hunting pressure (Table 1).

Estimating hunting pressure at a regional scale

We used the results of the regression modeling above to estimate hunting pressure across public lands in California hunting Zone A (North Unit 160), which spans multiple counties and ecoregions. We first restricted our study area by excising non-huntable areas from this region. We removed several land uses, including farmland, urban, commercial agricultural, and rural residential areas (California Department of Conservation 2018). We removed land ownerships including National Park Service, Air Force, and Department of Defense lands, and excluded any areas that were not publicly owned lands. We also removed bodies of water, as well as the Central Valley ecoregion, the habitat characteristics of which differ too greatly from our study site for meaningful predictions. Many public lands may have specific regulations regarding hunting, but we did not further examine specific properties, as our goal was to show potential rather than realized hunting pressure at this scale.

We used the estimates from the full and ARS regression models described above to project hunting pressure regionally. However, because some of the variables retained by our model selection were specific to the study site and not available at larger scales, we had to omit some data and redo model selection without them (Table 1). Additionally, for some model variables, we used a regionally available proxy instead of omitting the variable entirely (Supplementary Table 2). For example, distance to the protected BLM lands north of the study site was retained as a variable by regression model selection; as a regional proxy, we included distance to protected areas in general.

Additionally, we attempted to capture the variation in hunting pressure based on the inaccessibility of locations within this hunting zone. To do this, we divided the two regional projections we created by a raster of site "remoteness," defined as the travel time in minutes from the nearest populated center (Nelson 2008).

RESULTS

Hunter space use

We collected data from 302 hunters over a period of three years. Hunters spent an average of 9.3 hours in active hunting during their hunting day, and traveled an average of 21.9km total distance. Hunters spent the majority of their time close to roads on the site, with more than 60% of their time spent within 15m of roads (Figure 2).

Behavioral segmentation

Using first passage time (FPT) we partitioned hunter GPS data into two distinct behaviors: exploratory searching (ES) and area-restricted searching (ARS). Hunters spent 28.6% of their time in ARS, and the remaining time in ES. In both cases, hunters demonstrate characteristics of cursorial rather than sit-and-wait predators.

Estimating hunting pressure

We produced two models of hunting pressure informed by Brownian bridge movement modeling (Figure 3). Distinct peaks in hunting pressure are visible in these models. After reclassifying, 16.1% of the study site occurs in areas with high hunting pressure (greater than one standard deviation above the mean) for the full model, and 16.6% occurs in areas of high hunting pressure when only ARS data is included. One standard deviation below the mean identifies 19.6% and 19.1% of the site respectively using all data and only ARS data. Of 47 deer kill sites that were located between 2015 and 2017, 13 sites fall in areas of high hunting pressure according to the ARS model, and 2 fall in areas of low hunting pressure. By contrast, 25 of 47 sites occur in areas of high hunting pressure according to the full model, with no kill sites in areas of low hunting pressure.

We found a very low correlation between our model of hunting pressure and a previous, kill site derived model of hunting risk at the study site (Gaynor 2019). The R^2 for this regression was 0.246 for the full model, and 0.107 for the ARS model (Supplementary Figures 3&4).

Environmental covariates of hunting pressure

Model selection yielded a single top model for both ARS data and the full dataset of hunter GPS coordinates. Both models retained many of the same variables, including terrain ruggedness, road density, distances to the site boundary and to the adjacent BLM property, area of surrounding chaparral, coyote activity density derived from camera trap data, and distances to vegetation patch edges and to water (Table 1). The R^2 values for the regressions of the full model and ARS model respectively were 0.687 and 0.739

Estimating hunting pressure at a regional scale

We estimated potential hunting pressure at the regional level using both the full model and ARS model results (Figure 4, Supplementary Figure 5). Because not all variables were available for estimates at this regional scale, we had to rely on models from the study site that performed significantly worse than our top models, as measured using AIC. Nevertheless, R^2 values were similarly strong even when these variables were omitted (Table 1). In spite of differences in estimates of the strength of environmental covariates for the regression of the full and ARS models, the hunting pressure each predicts at a regional scale is noticeably similar. After scaling

and subtracting the ARS projection from the full model projection, we found little difference between these two outputs (Figure 4). These projections are both characterized by large areas of low predicted hunting pressure, with peaks in pressure tracing road networks across the region.

DISCUSSION

Roads across scales

Using an unprecedented combination of fine-scale GPS fix rates and comprehensive coverage of hunters, this study provides important insights into the movement ecology of the human "super predator" on public lands in California. Such fine-scale insights have important consequences for wildlife game species that have received too little attention (Rowcliffe et al. 2003; Papworth et al. 2012). Yet, given the level of detail and analytical methods available for this study, it was surprising to find the importance of roads at all scales of analysis. Even among individual hunters during area-restricted searches on foot, roads were a key predictor variable, and hunters spent more time on or near them than we anticipated. Across the study site, the cumulative effects of hunters moving across roads meant that this anthropogenic feature more than any of the site's natural features dictated the pattern of hunting pressure and shaped both the lethal and non-lethal consequences of hunting. At the regional level, much of the variation in hunting pressure that we projected is small compared to the more striking, bimodal pattern of pressure being high near roads and low away from them.

Links between the presence of roads and the lethal effects of hunting have been previously established at broad scales (Laurance et al. 2006; 2008), but here we show these connections mechanistically and at multiple scales of analysis. This has important implications. First, the fact that movement, and not just the lethal effects of hunting, are also tied to roads means that hunting's understudied non-lethal effects are also likely connected to the spatial patterning of road networks. By imposing hunting pressure on game species, road networks may alter game species behaviors, habitat selection, and even force them into ecological traps in which they encounter wild predators at greater rates (Lone et al. 2014). Second, our findings suggest that cursorial hunters, like those in this study, exhibit strong preferences for roads. This finding might be unsurprising for sit-and-wait hunters, but we show that even active area-restricted searches on foot have important ties to road networks, suggesting roads matter to hunting in multiple contexts. Finally, the conservation and management implications of hunter road use are far-reaching. Road networks in the region and across much of the world are currently rapidly expanding. Methods and technology are now available that show more clearly the extent of their lethal and non-lethal impacts and can allow managers and conservation practitioners simple and easily identifiable levers for regulating hunting.

In the sections below, we will discuss our findings in further detail at three scales mentioned: hunter behavior, site-wide hunting pressure, and projected potential regional hunting pressure.

Hunter behavior

Spatial analysis of hunter GPS data revealed a high percentage of time spent within short distances of roads (Figure 2). This finding confirmed our hypothesis and accorded well with other studies in different regions, suggesting that this pattern is widespread (Stedman et al. 2004; Lebel et al. 2012; Jones et al. 2017). Similarly, our hypothesis that hunters would avoid property

boundaries also proved correct, as is clear from analysis of raw GPS data (Figure 2) as well as from our site-level models of hunting pressure (Figure 3, Table 1), which show the corners of the property to be some of the least visited by hunters. This finding makes sense, as taking a position near the property boundary limits the available surrounding space in which hunting is legal. In this sense, the geometry of the legal landscape has important consequences for hunting, potentially creating refuges for target species, especially if neighboring properties have different management regimes (Adkins & Irby 1994).

Hunters did appear to be attracted to the neighboring BLM land (Table 1), however, likely due to the perception that this protected area would produce higher densities of deer on the study site. This behavior has been shown in other systems as well, where hunters aggregate near protected area boundaries to improve success (Tolon et al. 2012). In their responses to roads, boundaries, and protected lands, these behaviors suggest that hunters at our site conform well to patterns established across species and sites and thus suggest that findings of this study may be generalizable at larger scales.

In this system, as in others, first passage time appears to be a simple and effective tool for distinguish exploratory searching (ES) from area-restricted searching (ARS) (Fauchald & Tveraa 2003). This distinction allows for more precision in understanding the indirect effects of hunters as they move across the landscape. Studies have shown that game species, and deer in particular, are much more habituated to vehicles and show greater behavioral responses to humans on foot (Stankowich 2008). The ability to remotely identify where these behaviors occur should thus support more nuanced understanding of the spatial patterns of hunting pressure and the distribution of its non-lethal effects.

Hunters at our site exhibited cursorial behaviors, and behavioral segmentation did not identify any sit-and-wait behaviors. Sit and wait hunting is likely much more common on private lands where hunters may have multiple days to hunt and establish blinds or other ambush sites. However, our results suggest that hunters on public lands are likely to exhibit cursorial behaviors, as they may have limited hunting time and low site familiarity. In many cases, cursorial predators excite smaller risk responses from their prey than ambush predators (Preisser et al. 2007a; Thaker et al. 2011; Makin et al. 2017). This may suggest that the non-lethal effects of rifle hunting are mitigated on public compared to private lands in California.

Site-wide hunting pressure – environmental correlates

At the scale of our study site, roads again form an important predictor of site-wide hunting pressure. When we conducted regression on the full model of hunting pressure, roads stood out as the most influential variable (Table 1). While the viewshed from roads was not as significant a predictor of the pattern of hunting pressure, it was retained by model selection, ensuring that two road-related variables were included in the top regression model. We did not expect roads to remain as significant in the regression of the ARS model, as we predicted hunters would be leaving their vehicles to stalk deer on foot away from roads. However, while the strength of roads as an estimator did decrease in this regression, it remained an important part of this model as well.

Several other hypothesized predictors proved to be important in both the full model and the ARS model of hunting pressure (Supplementary Table 1, Table 1). Terrain ruggedness over a 1200-meter window was associated with reduced hunting pressure while greater viewsheds were associated with higher pressure, confirming our predictions that hunters would avoid rugged

areas where sightlines are shorter and access more challenging. Chaparral vegetation appears to have discouraged hunters in both models, as it is difficult to both see and walk through. Greater distances from vegetation patch edges was associated with increased hunting pressure, perhaps suggesting that hunters look for large patches of continuous vegetation in which noticing deer and movement is easier. We were surprised to see that distance from water was negatively associated with hunting pressure. Most water courses at our site occur in steep ravines, which we expected to deter hunters due to their enclosing vegetation, difficulty of access, and limited sightlines. However, like wild predators (Valeix et al. 2008), hunters may expect deer to occur near water sources, especially during August when temperatures at the study site soar and water is scarce. Finally, we were surprised to see that coyote activity density, as derived from a grid of camera traps, was retained as a model variable for both the full model and the ARS model. We predicted that high activity densities of coyote would reduce deer densities and activities, and that hunters would respond by moving elsewhere. Hunters may instead look for the same cues as coyotes in stalking deer, resulting in this positive association.

We expected greater differentiation between environmental correlates of exploratory searching and area-restricted searching on foot. While the strength of estimates differed between the full and ARS regression models, the models retained many of the same variables with similar strengths, and the signs of common variables were consistent across models (Table 1). This smaller than expected difference between the two models likely also attests to the importance of roads, as hunters stayed close to roads and the habitats associated with them in both behavioral states. On one hand, this potentially confounds inference, as the particular habitat characteristics surrounding roads at this specific study site are likely to be over-represented. On the other hand, it suggests that when making projections or inferences, roads are a relatively simple and highly explanatory proxy with a now established mechanistic backing in movement ecology.

Site-wide hunting pressure – relationship to mortality risk

A key finding at this scale was the poor correlation between our models of hunting pressure and previous risk models developed from historical kill locations at the study site (Gaynor 2019). Even among contemporary kill sites located during the study period, we found that the high hunting pressure (>1sd above the mean) areas of the full model overlapped with a greater number of deer kill sites than the ARS model. These findings imply that the non-lethal effects of hunting pressure, which result from hunter presence and movement, are surprisingly decoupled from mortality risk from hunting. Literature on space races between predators and prey makes clear that prey can quickly adapt their movement and ranges to predator presence (Sih 1984; Muhly et al. 2011), and deer specifically have been shown to rapidly adapt to hunting pressure (Karns et al. 2012; Little et al. 2014). However, managers have long relied strictly on kill counts at very broad scales (e.g., the large hunt zones of California) to regulate and manage hunting (Kuijper et al. 2013a). Our research suggests that even at finer scales, the locations of kill sites provide only a glimpse into the broader array of hunting effects. Non-lethal impacts from hunting pressure may follow significantly different patterns and predictors than lethal effects. With the methods and technology provided here, managers can better consider these effects in the future.

An alternative explanation for the better overlap between deer kill sites and the full model is that social attraction occurs between hunters on site. Social or group attraction has received attention recently in the movement ecology of wild populations of predators, such as baboons,

and works to identify group behaviors through analysis of movement data (Strandburg-Peshkin et al. 2018). For example, a group "leader" may identify a target prey or desirable hunting ground and eventually dictate the movements of a social group. At our site, hunters may hear from one another or from a posted map of kill sites about where successful harvest has occurred, and thus spend more time in exploratory driving at this site. In this way, the full model may show increased hunting pressure at kill sites, but this pressure may be an effect of previous successful kills rather than a cause for success. Future research can further interrogate hunter spatial data to understand patterns of group behavior as these methods continue to develop (Muscioni et al. 2019).

Spatial refugia from hunting pressure are clearly visible in both hunting pressure models, and few deer were killed in the lowest hunting pressure areas during the term of the study (Figure 3). However, by altering deer behavior, patterns of hunting pressure may force deer into ecological traps (Kilgo et al. 1998; Robertson & Hutto 2006). While rifle hunters appear to overlap with coyotes, mountain lions are the primary predator of black-tailed deer in the region (Wittmer et al. 2014). Mountain lions have been shown to be strongly avoidant of human activity, including road use (Smith et al. 2015; Wang et al. 2017). Thus, while deer may rapidly adapt to the spatial patterns of rifle hunting pressure, they may be forced into a tradeoff of facing greater exposure to wild predators. Further research that simultaneously tracks hunters, deer, and mountain lions can help provide answers to this important and fascinating "shell game."

This study showcases another important spatial refuge for deer: areas surrounding human development. In contrast to reported declines of deer across much of the western United States (CDFW 2019), deer are often considered a nuisance, occurring above social carrying capacity in urban and rural residential areas of California (Krausman et al. 2014). At this study site, the areas for which hunting is prohibited surround residences and research station offices. Where hunting is restricted here, a "human shield" is provided for deer (Berger 2007), not just against wild predators, but also against the lethal and non-lethal effects of hunters (Gaynor 2019). This study thus suggests that deer are unique as a game species in that they have adapted to use human shields against humans, which may partially explain their success in backyards even where declines are occurring in the wild.

Projected regional hunting pressure

While our findings at the individual and site level are meaningful, projecting these findings to larger scales likely has the most to offer conservationists and managers working on this topic. Our regional projection of hunting pressure contains nuanced variation within its predictions, but the overlap between these predictions and the regional road network is unmistakable. The distribution of data at this scale are approximately bimodal, with higher hunting pressure areas tracing existing roads in the region (Figure 4). Even though we were unable to use all of the environmental correlates determined in the site-level regression to build this model, it appears that this bimodal distribution is likely to persist regardless, minimizing the potential concerns of our estimation method when viewed at this scale. These conclusions may differ on private lands, where sit-and-wait hunting is more common, and so we have highlighted public lands as the most meaningful loci for predicting these data. For public land managers, these findings point to a simple and easy way to estimate the lethal and non-lethal effects of hunting: follow the roads.

Given the comparatively sparse distribution of roads in this region, the non-lethal effects of roads are likely to vary with use. Where road activity is high, game species are likely already

adapted in terms of behavior and habitat selection to the non-lethal effects of humans. However, if hunters take advantage of low-use roads, their non-lethal effects can be expected to be much higher. In both cases, ecological traps may occur during the hunting season. If hunting pressure surrounding roads is causing deer to face increased pressure from recovering mountain lion populations that avoid roads (Benson et al. 2016), even these non-lethal effects could contribute a mechanistic explanation to reported regional declines in deer populations (CDFW 2019).

While more research may indeed uncover the important non-lethal effects of road-centered hunting, this study region, and much of the western united states, has large inaccessible areas between its roads. Compared to the study site, much of this region features vast swaths of land that remain roadless. Deer home ranges in this region have also been reported to be some of the smallest of ever recorded (Wittmer et al. 2014), meaning that many individuals and even populations may not be exposed to intense hunting pressure at all, thus diminishing the strength of ecological traps via non-lethal effects. Here too, more research is needed to understand whether and how spatial refugia from hunting pressure away from roads are important to game species.

CONCLUSION

The movement ecology of the human super predator offers important insights into the manifold lethal and non-lethal effects of hunting. These analyses reveal hunters on public lands to maximize their time spent in active hunting modes. Hunters on these lands are cursorial, and, whether actively stalking on foot or exploring by car, they maintain a strong spatial association with roads. This association with roads persists when hunters are taken as a group at the study site, and reveals itself as an even stronger pattern when projected regionally. More than any natural feature, roads predict where hunting pressure will be highest, providing managers an easy proxy for broadly estimating and regulating the effects of hunting. While the importance of roads to hunting has long been argued for, we provide here a mechanistic connection that shows both the lethal and non-lethal consequences for deer in California. While further research of this nature is sorely needed in diverse contexts across the world, we expect that the findings presented here have broad relevance and help justify concerns over the ecological consequences of a rapidly expanding global road network.

FIGURE 1. This study was conducted at the Hopland Research and Extension Center in Mendocino County, California. This study site occurs near the geographic center of California hunt Zone A (North Unit 160) and hosts habitat types characteristic of the ecoregions occurring within this hunt zone. The site is served by a network of dirt roads emanating from a headquarters area where hunting is prohibited. Shown above are A) the study site boundary, constituent vegetation, road network and prohibited hunting areas, and B) the site's location within the Zone A (North Unit 160) hunting zone and larger ecoregions.

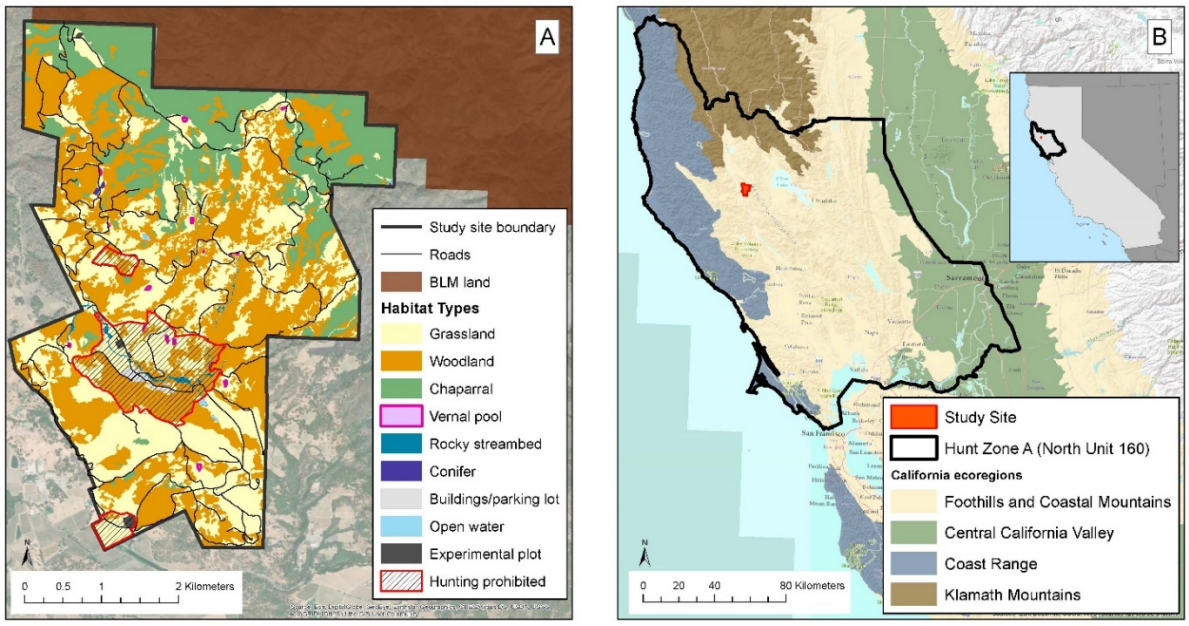


FIGURE 2. Hunter GPS points occurred across the study site, but there was a clear concentration around roads. More than 60% of all GPS points occurred within 15 meters of the site's road network. Points of area-restricted searching as defined by first passage time also occur throughout the site, and show a similar adherence to road networks. GPS points shown here have been subsampled to 600 seconds to improve legibility.

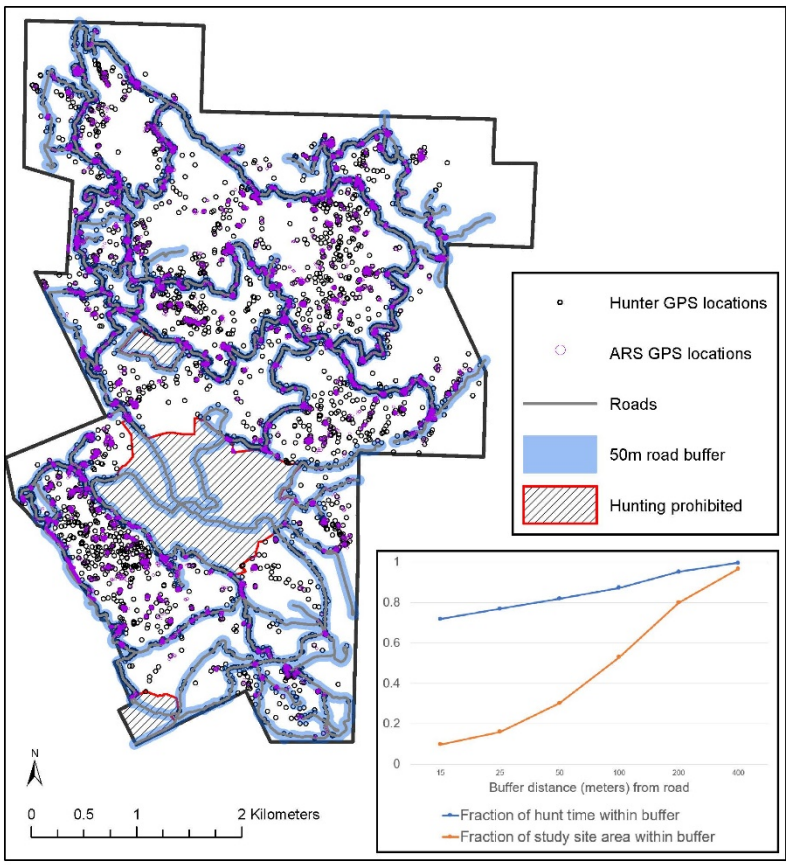


FIGURE 3. Brownian bridge movement models (BBMM) applied to hunter GPS data reveal peaks and valleys of hunting pressure. A) model produced from all GPS data, including both exploratory driving and area-restricted searching behaviors. B) model produced from only area-restricted searching behaviors. Areas greater than 1 standard deviation above mean hunting pressure are outlined in red. Sites of deer killed from 2015-2017 are also shown.

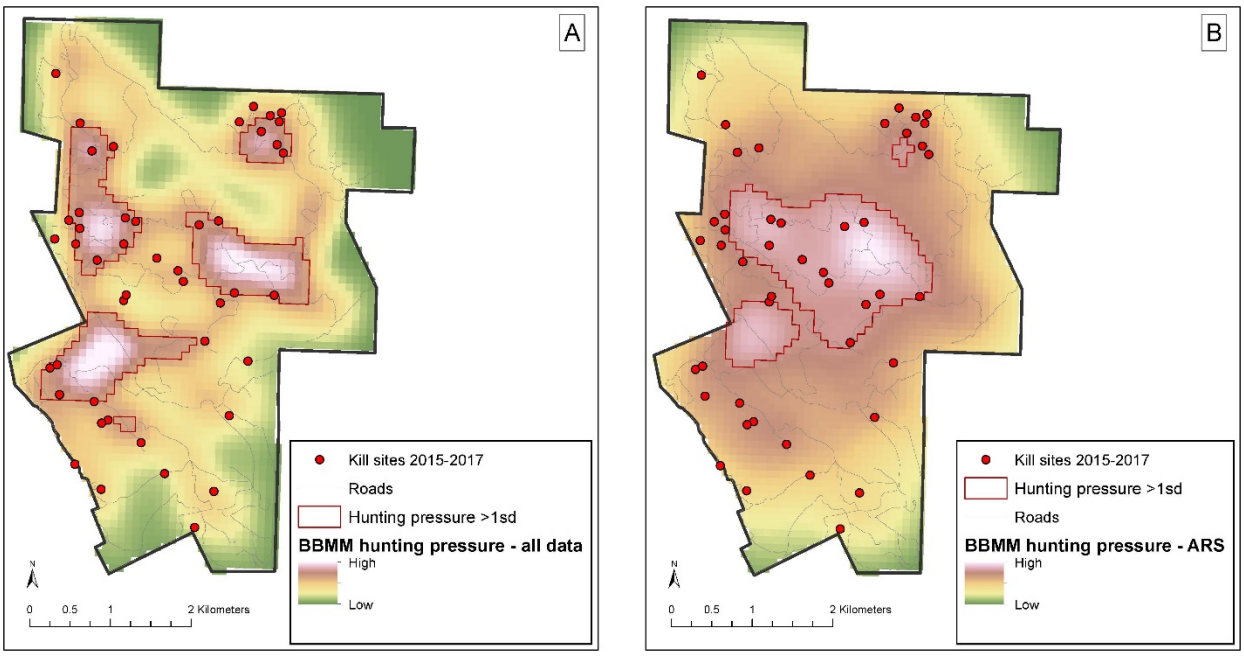


FIGURE 4. Estimated hunting pressure at the regional level. Using the regressions from our study site and regional environmental proxies, we projected potential hunting pressure across California hunt Zone A (North Unit 160). A) At the regional scale, variation in predicted hunting pressure exhibits a bimodal distribution, following roads. B) Variation in hunting pressure is clearer at smaller scales, but the pattern of the road network remains unmistakable. Because large areas in this hunt zone are not publicly owned lands, our projections are likely most accurate only for those public lands that permit hunting.

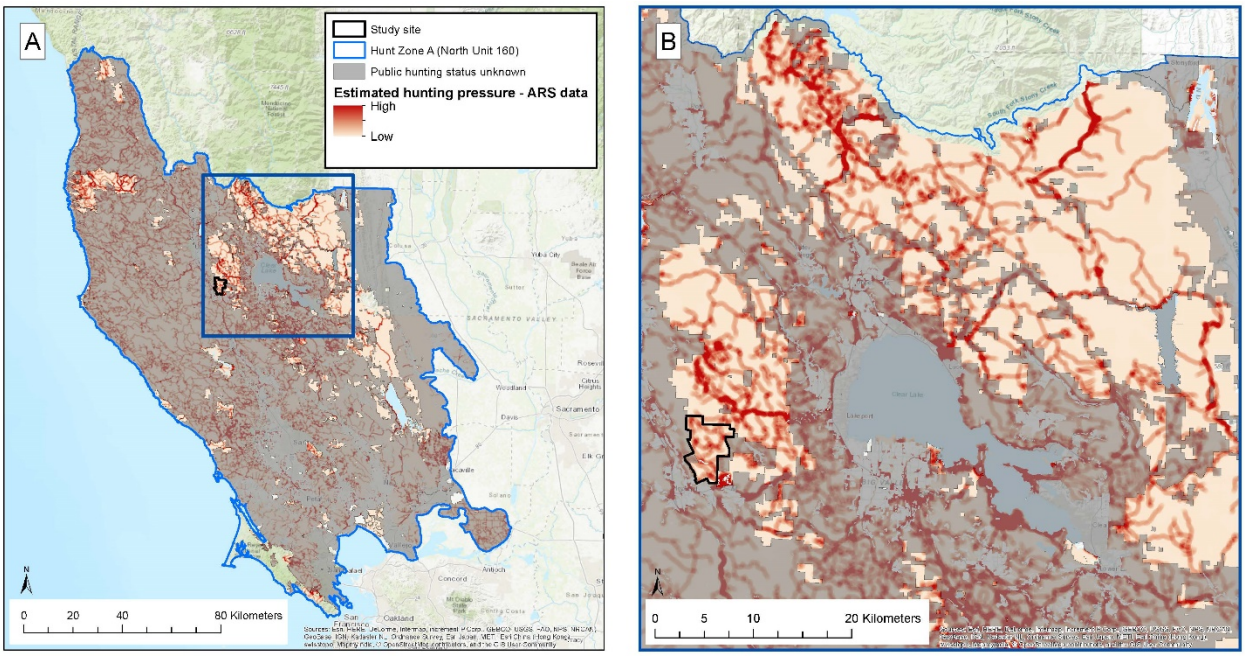
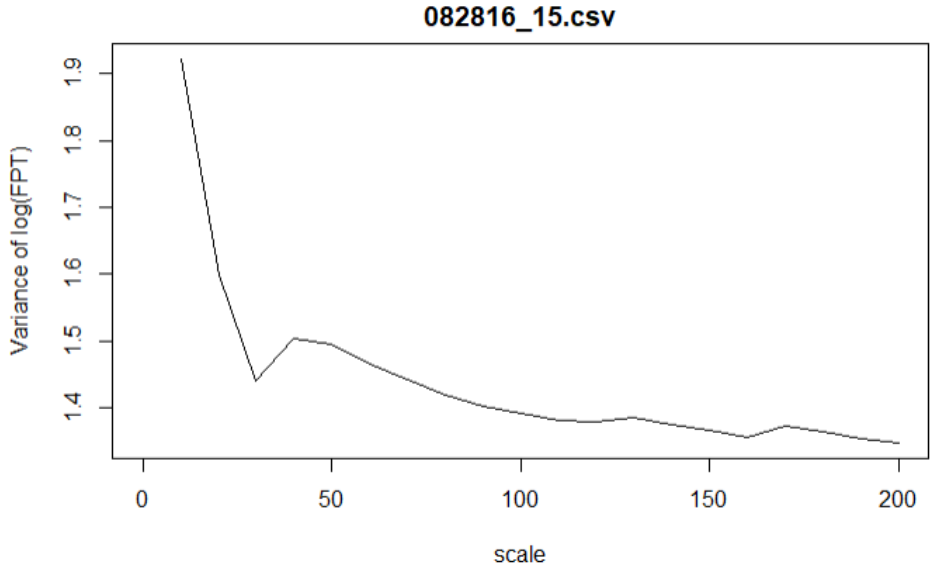


TABLE 1. VARIABLES ASSOCIATED WITH FOUR BROWNIAN BRIDGE MODELS OF SPATIAL HUNTING PRESSURE

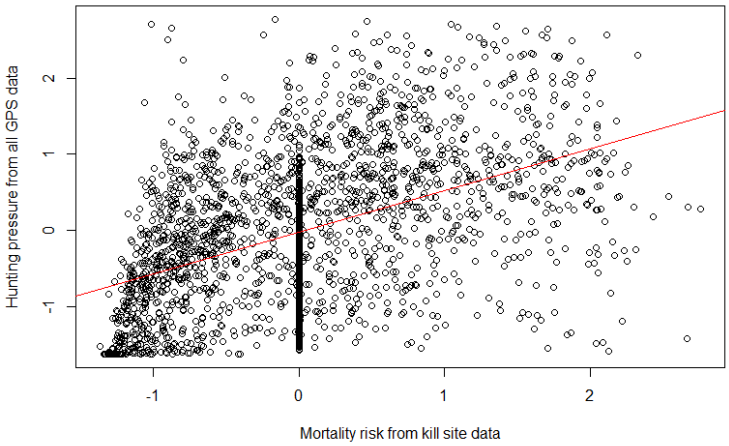
Regression using all hunter GPS data AIC = 3946, R^2 = 0.687				
Variable	**Estimate**	**Standard Error**	**t-value**	**p-value**
Intercept	-2.974e-15	1.158e-02	0.000	1.00000
Ruggedness (1200m window)	-1.086e-01	1.479e-02	-7.340	2.94e-13
Viewshed from road	2.962e-02	1.288e-02	2.299	0.02157
Road density	6.179e-01	1.302e-02	47.464	< 2e-16
Distance to site boundary	2.061e-01	1.298e-02	15.885	< 2e-16
Distance to BLM land	-2.661e-01	1.831e-02	-14.532	< 2e-16
Chaparral within 120m	-2.602e-01	1.755e-02	-14.830	< 2e-16
Coyote activity density	3.803e-02	1.298e-02	2.929	0.00343
Distance to vegetation patch edge	3.381e-02	1.268e-02	2.667	0.00771
Distance to water	-7.479e-02	1.432e-02	-5.223	1.92e-07
Regression using all hunter GPS data and variables available for regional estimation AIC: 3953, R^2 = 0.686				
Variable	**Estimate**	**Standard Error**	**t-value**	**p-value**
Intercept	-2.873e-15	1.160e-02	0.000	1.00000
Ruggedness (1200m window)	-9.926e-02	1.447e-02	-6.860	8.81e-12
Viewshed from road	3.121e-02	1.289e-02	2.422	0.01552
Road density	6.215e-01	1.298e-02	47.883	< 2e-16
Distance to site boundary	2.019e-01	1.292e-02	15.631	< 2e-16
Distance to BLM land	-2.529e-01	1.777e-02	-14.228	< 2e-16
Chaparral within 120m	-2.536e-01	1.743e-02	-14.551	< 2e-16
Distance to vegetation patch edge	3.682e-02	1.266e-02	2.909	0.00366
Distance to water	-7.300e-02	1.433e-02	-5.094	3.78e-07
Regression using ARS data only AIC: 3523, R^2 = 0.739				
Variable	**Estimate**	**Standard Error**	**t-value**	**p-value**
Intercept	-2.951e-15	1.058e-02	0.000	1.000000
Ruggedness (1200m window)	-3.488e-01	1.348e-02	-25.869	< 2e-16
Distance to fence	-9.403e-02	1.187e-02	-7.921	3.62e-15
Road density	1.538e-01	1.161e-02	13.249	< 2e-16
Distance to site boundary	5.037e-01	1.204e-02	41.823	< 2e-16
Distance to BLM land	-3.331e-01	1.682e-02	-19.811	< 2e-16
Chaparral within 120m	-2.023e-01	1.611e-02	-12.557	< 2e-16
Coyote activity density	1.158e-01	1.189e-02	9.742	< 2e-16
Distance to vegetation patch edge	4.031e-02	1.159e-02	3.477	0.000516
Distance to water	-2.022e-01	1.310e-02	-15.435	< 2e-16
Regression using ARS data and variables available for regional estimation AIC: 3684, R^2 = 0.720				
Variable	**Estimate**	**Standard Error**	**t-value**	**p-value**
Intercept	-2.836e-15	1.096e-02	0.000	1.000000
Ruggedness (1200m window)	-3.243e-01	1.363e-02	-23.798	< 2e-16
Road density	1.884e-01	1.162e-02	16.213	< 2e-16
Distance to site boundary	4.731e-01	1.220e-02	38.790	< 2e-16
Distance to BLM land	-2.694e-01	1.665e-02	-16.177	< 2e-16
Chaparral within 120m	-1.952e-01	1.645e-02	-11.870	< 2e-16
Distance to vegetation patch edge	4.404e-02	1.194e-02	3.688	0.000231
Distance to water	-1.913e-01	1.353e-02	-14.133	< 2e-16

SUPPLEMENTARY FIGURE 1. We used small, commercially available GPS units to track hunters at our site. These units (i-gotU GT-600) were small enough to carry without altering hunter behavior, had suitable battery life and memory, and could collect points at high fix rates (10s in our study).

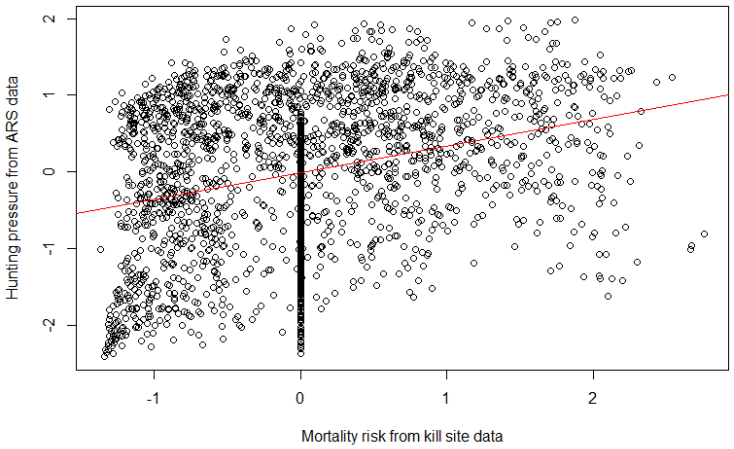
SUPPLEMENTARY FIGURE 2. Example of graph of variance of the log of first passage time (FPT) against FPT radius. There is a characteristic peak at approximately 40 meters.



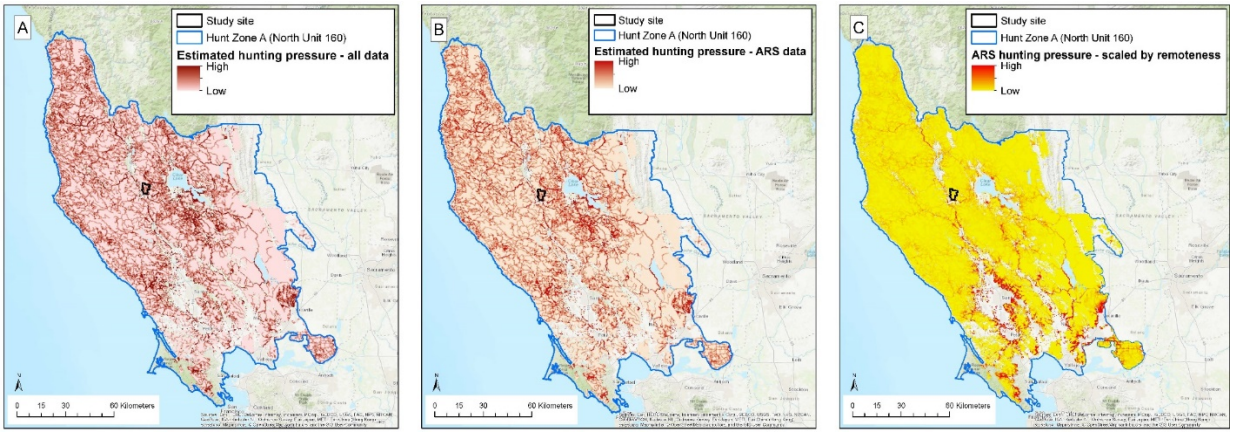
SUPPLEMENTARY FIGURE 3. Regression of a previously conducted study of mortality risk derived from historical kill sites against the hunting pressure model using all GPS data. The R^2 for this regression was 0.246.



SUPPLEMENTARY FIGURE 4. Regression of a previously conducted study of mortality risk derived from historical kill sites against the hunting pressure model using only area-restricted search (ARS) data. The R^2 for this regression was 0.107.



SUPPLEMENTARY FIGURE 5. We used estimates from both our A) full and B) ARS models of hunting pressure to scale up findings to the regional level. While there was variation across these regional projections, both models show a bimodal distribution of hunting pressure near and far from roads. Even when we C) scaled hunting pressure by the remoteness of location, this bimodal distribution persisted.



SUPPLEMENTARY TABLE 1. ENVIRONMENTAL VARIABLES USED TO CONDUCT REGRESSIONS ON BROWNIAN BRIDGE HUNTING PRESSURE MODELS

All GIS data was provided by the Hopland Research and Extension Center (HREC). The authors created habitat type data from aerial basemaps provided by HREC, and ground-truthed 50 random control points to ensure accuracy. Coyote activity density was calculated using a grid of 36 camera traps deployed at the study site by the authors.

Variable	Category	Hypothesized effect on hunting pressure	Resolution
Area of chaparral within 120m	Habitat	Negative. We expect the low visibility of chaparall to deter hunters and lower pressure	10m
Area of grass within 120m	Habitat	Positive. We expect the high visibility within grassland to attract hunters and increase pressure	10m
Area of woodland within 120m	Habitat	Negative. We expect the middling visibility of woodlands to deter hunters and lower pressure	10m
Coyote activity density	Habitat	Negative. We expect coyote activity to reduce deer presence, and that hunters will track deer density, resulting in lower hunting pressure	Derived from a camera grid spaced hexagonally 750m apart
Distance to BLM	Habitat	Negative. We expect hunters to spend more time near BLM protected land, as shown in other studies, increasing pressure	10m
Distance to vegetation patch edge	Habitat	Negative. We expect hunters to focus efforts in large patches away from edges where contrasts are high, decreasing pressure near patch boundaries	10m
Distance to vernal pools	Habitat	Negative. We expect hunters to focus time near (dry) vernal pools where they may expect deer to congregate, increasing pressure	10m
Distance to water	Habitat	Positive. We expect hunters to avoid the steep ravines in which water sources occur, increasing pressure at distance from water	10m
NDVI	Habitat	Negative. We expect hunters to avoid denser vegetation where visibility may be comparatively low, decreasing pressure.	10m
Distance to nearest fence	Human infrastructure	Negative. We expect hunters to increase pressure near fences where deer flight paths may be restricted.	10m
Distance to no hunt zone	Human infrastructure	Positive. We expect hunters to avoid the no hunt zone to increase the angles and distances at which they may hunt, increasing pressure away from this zone.	10m
Distance to site boundary	Human infrastructure	Positive. We expect hunters to avoid site boundaries to increase the angles and distances at which they may hunt, increasing pressure away from this zone.	10m
Road density	Human infrastructure	Positive. We expect hunters to spend more time on or near roads, increasing hunting pressure.	10m

Variable	Category	Hypothesized effect on hunting pressure	Resolution
Ruggedness – 1200m window	Topography	Negative. We expect hunters to avoid more rugged terrain where sight lines and access are difficult, reducing pressure.	10m
Ruggedness – 250m window	Topography	Negative. We expect hunters to avoid more rugged terrain where sight lines and access are difficult, reducing pressure.	10m
Ruggedness – 30m window	Topography	Negative. We expect hunters to avoid more rugged terrain where sight lines and access are difficult, reducing pressure.	10m
Ruggedness – 500m window	Topography	Negative. We expect hunters to avoid more rugged terrain where sight lines and access are difficult, reducing pressure.	10m
Ruggedness – 800m window	Topography	Negative. We expect hunters to avoid more rugged terrain where sight lines and access are difficult, reducing pressure.	10m
Viewshed from roads	Topography	Positive. We expect hunters to spend more time on roads where viewsheds area large, increasing pressure	10m

SUPPLEMENTARY TABLE 2. LIST OF PROXY VARIABLES USED TO PROJECT SITE-LEVEL HUNTING PRESSURE AT THE REGIONAL SCALE.

Regression variable	Variable used for regional estimate	Proxy source
Ruggedness (1200m window)	Ruggedness (1200m window)	Derived from 30m DEM from USGS
Viewshed from road	Viewshed from road	Calculated from TIGER road data and 30m DEM from USGS
Road density	Road density	Calculated line density in a 300m window from TIGER road data
Distance to site boundary	Distance to management change	Calculated Euclidean distance from changes in government property ownership (BLM data) or land use (FMMP data)
Distance to BLM land	Distance to protected land	Calculated from California Protected Areas Database superunits
Chaparral within 120m	Chaparral within 120m	Calculated from FRAP's fveg15 data
Distance to vegetation patch edge	Distance to vegetation patch edge	Calculated from FRAP's fveg15 data
Distance to water	Distance to water	Calculated from CDFW's tertiary stream database

Chapter 3. Patterns of coyote predation on sheep in California: A socio-ecological approach to mapping risk of livestock-predator conflict

ABSTRACT

Conflict between livestock producers and wild predators is a central driver of large predator declines and simultaneously may imperil the lives and livelihoods of livestock producers. There is a growing recognition that livestock-predator conflict is a socio-ecological problem, but few case studies exist to guide conflict research and management from this point of view. Here we present a case study of coyote-sheep predation on a California ranch in which we combine methods from the rapidly growing field of predation risk modeling with participatory mapping of perceptions of predation risk. Our findings reveal an important selection bias that may occur when producer perceptions and decisions are excluded from ecological methods of studying conflict. We further demonstrate how producer inputs, participatory mapping, and ecological modeling of conflict can inform one another in understanding patterns, drivers, and management opportunities for livestock-predator conflict. Finally, we make recommendations for improving the interoperability of ecological and social data about predation risk. Collectively our methods offer a socio-ecological approach that fills important research gaps and offers guidance to future research.

INTRODUCTION

Conflict between livestock producers and wild predators has been an intractable problem for millennia, with high stakes for both people and wildlife (Linnell et al. 2012). A globally-expanding human footprint ensures that predators and livestock continue to encounter one another on landscapes increasingly defined by scarcity, further intensifying conflicts (Ogutu et al. 2016; Kuijper et al. 2016; Wolf & Ripple 2017; Drouilly et al. 2018). For livestock producers, the presence of predators on a landscape often poses a material threat to lives and livelihoods, leading to preemptive or retaliatory killing of predators (Scrivner & Conner 1984; Treves & Karanth 2003; Graham et al. 2005; Muhly & Musiani 2009; Mishra et al. 2016; Widman & Elofsson 2018). These killings hasten the decline of large predators throughout the world and, combined with other drivers of loss, threaten their continued existence (Ripple et al. 2014). Large predator declines have far-reaching consequences, as their disappearance can trigger drastic ecosystem alterations and collapse (Estes et al. 2011) or engender social conflict (Brashares et al. 2014). While research has traditionally considered livestock-predator conflict from within disciplinary boundaries, there is a growing recognition that it is fundamentally a socio-ecological phenomenon, in which human beliefs and practices are reciprocally intertwined with ecological processes (Woodroffe et al. 2005; Manfredo 2008). Important theoretical groundwork has been laid, but there remains an important need for case studies that test socio-ecological methods for understanding livestock-predator conflict (Dickman 2010).

The risks of livestock predation in space – both actual and perceived – are critical components of livestock-predator conflict with important potential to link its social and ecological dimensions. There exists a rich body of literature on the ecology of predation risk developed in natural systems (Sih 1984; Hebblewhite et al. 2005; Laundre 2010; Gaynor et al. 2019). Ecologists have demonstrated that heterogeneous environments produce differential risks

of predation, and that habitat characteristics, topography, ambush points, and other such landscape features are essential to the spatial patterning of predation risk (Brown 1999; Trainor et al. 2014; Gaynor et al. 2019). More recent research has applied these ecological theories to livestock predation (Kluever et al. 2008; Shrader et al. 2008; Kluever et al. 2009; Laporte et al. 2010; Wilkinson et al. 2019). In particular, the rapidly growing field of predation risk modeling uses statistical approaches from wildlife ecology to generate predictive, spatially explicit maps of livestock predation risk as it varies over a landscape (Treves & Naughton-Treves 2004; Miller 2015). Predation risk modeling is an especially suitable component of a socio-ecological case study as it is designed to be easily interpretable and actionable by producers and conservation practitioners, and its outputs are readily commensurable with quantitative social data (Suryawanshi et al. 2013; Miller 2015; Miller et al. 2016).

To understand the social dimensions of risk, it is critical to expand research on the risk perceptions of livestock producers (Treves et al. 2006; Dickman 2010; Marchini & Macdonald 2012; Suryawanshi et al. 2013; Kansky & Knight 2014; Treves & Bruskotter 2014). The conservation and recovery of large predators throughout the world will depend as much on perceptions and tolerance of them as the material risks they pose (Treves & Karanth 2003; Behr et al. 2017). Here we define "risk perceptions" as the set of beliefs held by a producer regarding the spatial variation in riskiness of the production landscape in terms of predation. Studies may rely entirely on perceptions to understand spatial patterns of livestock predation risk when other data is unavailable (Broekhuis et al. 2017), and participatory maps of human wildlife conflict have formed an increasingly important part of research and management toolkits for mitigating conflict (Treves et al. 2006; Kahler et al. 2012). These risk perceptions may (Miller et al. 2016) or may not (Suryawanshi et al. 2013) align well with empirical observations of predation likelihood, such as those produced by the predation risk models described above. Regardless of their accuracy, perceptions of risk are among the most important drivers of livestock husbandry decisions, including retaliatory actions against predators (Marchini & Macdonald 2012; Scasta et al. 2017; Moreira-Arce et al. 2018). Risk perceptions thus form critical components of producer decisions that actively shape the spatial pattern of predation risk by delimiting where livestock, and thus predation, may occur.

Predation risk is thus a function of both ecological characteristics and human decisions and the interactions between the two, meaning that an accurate understanding of livestock predation risk patterns must be gained through a socio-ecological lens. Ecological studies of livestock predation are still in need, and have important potential to reveal blind spots for livestock producers and managers regarding the circumstances and drivers of conflict (Wilkinson et al. 2019). However, strictly ecological approaches may suffer from selection bias, in which available data do not represent the system, if they do not explicitly incorporate producer decisions regarding the distribution of livestock, and thus livestock predation. This is likely a widespread yet underappreciated methodological issue, as we have found no other studies describing it in the literature. Simultaneously, better approaches for quantifying risk perceptions and making them consistent with ecological models is a critical need for socio-ecological understandings of conflict (Dickman 2010). We have also found no studies that have explicitly tested methods for improving interoperability between social and ecological data on predation risk. These notable research gaps stress the need for research that approaches livestock-predator conflict from a comprehensive, socio-ecological point of view.

Here we present a case study on predation of domestic sheep (*Ovis aries*) by coyote (*Canis latrans*) in California that demonstrates the complementarity of social and ecological approaches to studying livestock-predator conflict and the cost of omitting either from consideration. First, we constructed fine-scale predation risk models using a unique 10-year dataset of livestock predation locations to examine environmental correlates of predation and produce a predictive map of predation risk. Second, we conducted a participatory mapping exercise with livestock producers to quantify and map producer risk perceptions. Third, we administered a questionnaire to the same producers to quantify perceived environmental drivers of predation risk. Finally, we compared the maps produced by each of these exercises to reveal the concordances and discrepancies between them, and, more importantly, to show the critical importance of socio-ecological approaches like this one to future conflict research.

METHODS

Study area

We focused our research on coyote-sheep conflict in California, United States. As a pastured animal, sheep provide a particularly strong example of the role of husbandry decisions in determining predation risk. While cattle are too large to be prey for many local predator species, 28% of adult sheep losses and 36% of lamb losses in the USA in 2014-2015 were attributed to predators, and primarily to coyotes (USDA 2015). California is the second-largest sheep producing state in the United States, and predation risk is a growing concern locally. After centuries of persecutions and extirpations (Reynolds & Tapper 1996), a series of economic, legal, and cultural changes in California have led to large predator recoveries in the past few decades, heightening concerns about conflict (Berger 2006; Bergstrom 2017; Scasta et al. 2017). Coyotes have recovered more rapidly than other large predators, and their generalist diet and adaptability as predators have enabled the species to flourish in human-dominated spaces. These characteristics of predator, prey, and site make coyote-sheep conflict in California an ideal case study site for examining conflict in the 21st century.

We conducted our study at the University of California's 5,358 acre Hopland Research and Extension Center (HREC), located in the Mayacamas Mountains in Mendocino County, California. HREC lies between rural agricultural production and wildlands, bounded by remote Bureau of Land Management lands to the north and vineyards and suburban residences to the south. A mosaic of representative California Coast Range habitat types occurs on the property, including grasslands, oak woodlands, and chaparral (Figure 1).

Both coyotes and sheep occur at this site. Before the study site was donated to the University of California in 1951, HREC was a sheep ranch, and the university has maintained sheep on the site since its acquisition. During our study, 600 sheep on the site routinely grazed 34 of HREC's 60 total pastures. Pastures at HREC range in size from 3 to 263 hectares, and are enclosed by fences of varying types, heights, and ages. Though other large predators including black bears (*Ursus americanus*), mountain lions (*Puma concolor*), and bobcats (*Lynx rufus*) occur on the site, coyotes account for the vast majority of all livestock predation, with estimates up to 98% (Scrivner et al. 1985; Conner et al. 1998; Neale et al. 1998; Blejwas et al. 2002; Jaeger 2004). We reviewed logs recorded by livestock producers covering the past 50 years of husbandry and found no confirmed predations by any species except coyote. Furthermore,

neither staff nor agents of Wildlife Services contracted by HREC consider any other species as threats to the sheep at this site.

Mapping Observed and Perceived Predation Risk

To form a socio-ecological understanding of predation risk at the study site, we employed multiple modes of analysis, using maps as a commensurable format for quantifying and comparing these spatially-explicit approaches. First, we built predation risk models following the principles of resource selection functions to identify correlates of predation sites and make predictions about the spatial distribution of observed risk. Second, we developed participatory risk perception maps drawn by producers that represented their risk perceptions across the site's extent. Finally, we administered a questionnaire to examine how producers linked environmental and husbandry features to their risk perceptions, and we produced a map based on the answers provided in this exercise.

Predation Risk Models of Observed Risk

Data Collection

We built predation risk models using livestock predation data collected by livestock producers since 2008. At HREC, when producers suspected a sheep predation has occurred, they filled out a data sheet detailing the location and time of the kill, the predator suspected, and whether enough evidence was available to confirm the species of predator. Producers marked carcass locations on a topographic map with 10 m contour intervals and demonstrated excellent knowledge of the geography of the site. When we validated 10 test sites by returning to them with a GPS, we found mapped carcasses to be within the GPS error (10 m) of their reported location.

In this analysis, we included only livestock predations for which producers felt there was sufficient evidence to confirm the predator species. Additionally, we excluded events in which producers did not provide a spatial location or in which confidence in that location was low (e.g., signs of a carcass being dragged after the kill). This filtering yielded n = 91 predation events.

We created a database of 40 variables describing the environment at and around the site of each predation event (Supplementary Table 1). We included variables that we hypothesized to affect the spatial pattern of predation risk based on existing research on coyote-sheep predation and discussions with producers at the study site. We included human presence and husbandry, topography, habitat, and pasture characteristics. We imported all data to ArcGIS as either 10 m rasters or pasture-level vectors (Supplementary Table 2; ESRI 2018). This resolution reflected the approximate error expected in the location of predation events by staff, and the use of data at this resolution allowed us to explore fine-scale variation in patterns of attack likelihood.

Statistical Modeling

Following methods from other predation risk modeling studies (Treves et al. 2011; Miller 2015) we built predation risk models based on the approach of resource selection functions (Boyce et al. 2002). Resource selection functions typically predict animal habitat use based on a logistic regression comparing "use" locations drawn from observations or telemetry to "non-use" locations, where animals could have but did not occur. In our case, "use" locations were the 91 sites of sheep predation by coyotes, and "non-use" locations were 600 randomly generated points

(using the Create Random Points tool in ArcGIS) occurring within pastures where sheep were grazed.

We modeled attack likelihood from the use and non-use points based on the 40 variables collected at each site using logistic regression in the program R (R Core Team 2018). We used the `glmer` function in the lme4 package and included pastures as a random effect in our analysis to account for differences in pasture residence times. We used a hypothesis-driven approach to winnow down our large number of variables. We grouped variables thematically into categories of human presence and husbandry, topography, habitat, and pasture characteristics. We used model selection in a maximum likelihood framework to determine the most influential variables within each group (Burnham and Anderson 2002). We maintained all variables that were included in models within 2 delta AIC of the top model. We then combined these variables into a single model, and again used a maximum likelihood model selection approach to rank models. When we excluded non-converging models, a single top model remained, which was also the most parsimonious model. We calculated a variance inflation factor for all retained variables and confirmed that multicollinearity was not present in retained variables.

We tested the robustness of this model by bootstrapping a calculation of the area under the receiver operating characteristics curve (AUC) (Pearce & Ferrier 2000). We split the data, with 80% as training and 20% as testing data, and calculated the AUC 100 times using the `performance` function in the ROCR package in R, generating a range of values, a mean, and a standard deviation for assessing goodness of model fit.

Using the `predict` function in the car package in R, we mapped the results of this model across the extent of the study site. We reclassified the resulting 0-1 risk probabilities using two different schemes: an equal interval classification with low (0 – 0.33), medium (0.33 – 0.67) and high (0.67 – 1.0) values and a geometric interval with low (0 – 0.11), medium (0.11 – 0.33), and high (0.33 – 1.0) values. We initially chose an equal interval classification to match the format in which we asked livestock producers to share their perceptions of risk (described below). However, our initial results suggested that producers might have a low tolerance for risk, making a geometric interval that allows for more high-risk areas a better model analog.

Our discussions with producers led us to hypothesize that risk perceptions might be driven by the riskiest sites in a given pasture. Thus, we also created a coarser model at the pasture level in which risk across an entire pasture was defined by the riskiest 10m cell within it.

Participatory Maps of Risk Perceptions

We invited all 10 available current and former livestock producers at the study site to map their risk perceptions across the study site, in both grazed and ungrazed pastures. We recognize that this sample size is perhaps not large enough to represent the full variation of perceived risk across producers in the region. However, it likely captures well the experience of producers making management decisions at the study site and suitably demonstrates our general approach. Of the producers invited to participate, nine agreed and one declined. We first conducted unstructured interviews with each producer. These interviews informed the breadth of variables included in our predation risk model (described above), established rapport with the producers, and primed them to think about how attack likelihood varies in space.

We presented each producer with a 150 cm x 75 cm hardcopy map of the study site showing a high-resolution aerial imagery base map, pasture boundaries, roads, and other major identifying landmarks. We asked producers to draw areas of high, medium, and low risk for

sheep with regard to coyote predation using red, yellow, and green permanent markers respectively (Supplementary Figure 1). We clarified that these categories should be proportional to one another, such that they might be translated to a scale ranging from 1 to 3. We allowed interviewees to include as much detail in their maps (i.e., at any spatial resolution) as they felt necessary to represent risk gradations across the landscape. We digitized these hand-drawn perception maps in ArcGIS and assigned each color a score of 1 (low risk), 2 (medium risk), or 3 (high risk). We combined these individual maps into a summary raster at 10m resolution, with each cell representing the mean risk score across all interviewees.

We also identified environmental correlates for this summary risk perception map. Using ArcGIS, we generated 2,000 random points at the study site, each with a value (1, 2, or 3) drawn from the summary risk perception map. We conducted linear regression and model selection with the 40 environmental variables described above and in Supplementary Table 1 to determine what environmental features were most strongly associated with perceptions of predation risk.

Questionnaire

To further explore the drivers of perceptions of predation risk, we sent a follow-up questionnaire to all producers we interviewed. We presented them with a list of environmental and husbandry features that had been mentioned in unstructured interviews or retained by our predation risk model. We asked them to rank on a 1-5 scale from not important to ci how influential each feature was in determining the predation risk of a site. We summarized these results and used them as weights to produce a 10 m raster layer that represented a questionnaire-based spatial model of perceived risk. As with our predation risk model, we reclassified the range of values produced in this exercise using both equal interval and geometric interval classification schemes to compare their fit with the participatory maps of risk perception.

Comparing Approaches

We classified data across these three approaches (predation risk modeling, participatory perception maps, and questionnaire) into the same categories of low (1), medium (2), and high (3) risk. This enabled us to directly compare differences across these three models by subtracting one model from another using the raster calculator in ArcGIS. This exercise produced 10m raster layers with values ranging from -2 to 2. A value of 0 indicates agreement between models; negative values indicate that perceptions show higher values of risk than the compared model; positive values indicate that perceptions show lower values of risk than the compared model.

RESULTS

Predation Risk Models

The top predation risk model retained ten variables (Table 1 and Supplementary Table 2). Our bootstrapped AUC results ranged from 0.72 to 0.94, with a mean value of 0.86 and a standard deviation of 0.04, indicating a strong model fit (Pearce & Ferrier 2000).

When we used this model to predict the spatial variation in predation likelihood across the study site, we found that most of the site was scored as low risk (Figure 2). When an equal interval classification was used, 96.0% of the site received a score of 1 (low risk), 3.8% of the site received a score of 2 (medium risk), and only 0.2% received a score of 3 (high risk). When a geometric interval was used, there was a larger percentage of high (4.0%) and medium (28.3%)

scores on the site, but low risk areas (67.7%) still dominated. Both of these maps identify a few salient high-risk features, including steep-sided ravines highlighted in the blowup maps in Figure 2.

Participatory Perception Maps

In contrast with the results of the predation risk models above, the summary risk perception map codes the large majority of our study site as high risk (Figure 3). This summary map scores 82.1% of the study site as high risk, 14.1% as medium risk, and 3.8% of the site as low risk. Only 7 of the study site's 34 grazed pastures are coded as predominantly high risk in this summary perception map. Only one pasture that is not currently grazed is coded as predominantly medium risk, and none of the ungrazed pastures are coded as predominantly low risk (Figure 3). Producers were largely in consensus with their designations of perceived risk, with only a few areas of disagreement occurring in some of the more frequently grazed pastures.

Linear regression modeling of the summarized participatory map produced a parsimonious model which retained only four variables (Table 1). Pasture size was by far the variable most strongly associated with high risk perceptions. Pastures with more guard dogs and a higher proportion of grassland were associated with lower risk perceptions, while ruggedness within 30m was associated with higher risk assignments.

Questionnaire

Mean questionnaire scores (Table 1) indicated that producers roundly regarded the number of guard dogs in a pasture as the most important factor in determining predation risk (mean score 4.8 out of 5). Producers also gave high scores to ruggedness within a 30 m window (3.7) and 500m window (3.6), as well as to the proportion of chaparral (4.0) and grassland (4.0) in a pasture. The condition (3.8) and height (3.4) of the nearest fence also received high mean scores. While producers scored pasture size highly (3.7), it did not rank at the top of variables in this questionnaire as it did in the linear regression of the participatory map scores.

As with the predation risk model results above, we found stark differences in mapping the results of questionnaire scores at a 10 m resolution using an equal interval compared with a geometric interval. The former coded most of the study site as low or medium risk with only small pockets of high risk, while the latter displayed only a few areas of low risk among large areas of medium and high risk (Figure 4). The questionnaire scores we mapped at the pasture scale yielded larger areas of high and low risk, with medium risk covering a smaller area compared to the 10 m resolution map (Figure 4).

Comparison of Models and Perceptions

There were stark differences between the predation risk models and the summary participatory risk map (Figure 5). Even when we applied a geometric interval, only 8.7% of our study site showed agreement (a difference of 0) between these two maps (Figure 5A). Across 57.0% of the study site, perceptions indicated high risk where the predation risk model indicated low risk (a difference of +2), and only 3.0% of the site featured predation risk model scores that were higher than perceptions (differences of -1 or -2; Figure 5A). When we applied the highest predation risk model score to its entire containing pasture, we found much higher areas of agreement with perception maps (Figure 5B). Using the predation risk model reclassified by geometric interval, we found that areas with a difference of 0 cover the majority of the study site (81.2%), while

strong disagreement (differences of -2 or +2) was comparatively rare (3.2% and 0.9%, respectively).

Mapped questionnaire scores showed large areas of agreement with the summary perception map (Figure 5). When mapped at a 10m resolution using a geometric interval to reclassify results, we found 62.0% of our study site had a difference of 0, and less than 1.0% showed strong differences of -2 or +2 (Figure 5C). Questionnaire scores mapped at the pasture level showed even larger areas of agreement with perception maps, with 75.0% of the study site having a difference of 0. Strong differences of -2 or +2 were also rare (<1.0%; Figure 5D). Agreement was most widespread in ungrazed pastures, while grazed pastures had greater areas of difference, including the only pasture with a majority of its area characterized as +2.

DISCUSSION

This case study examines novel approaches by which to combine ecologically-driven predation risk models and producer risk perceptions. The similarities and differences between the multiple maps we produced demonstrate the complexity of understanding livestock predation risk and the utility in applying socio-ecological approaches to managing human-wildlife conflict. Our results contribute several important findings, both in terms of specific management takeaways for the study site and broader guidance for future research and management of conflict from a socio-ecological perspective. The strong contrast between predation risk models and producer maps of risk perceptions highlights shortcomings of relying solely on either approach, demonstrates opportunities for applying these approaches in tandem, and reveals an important but often overlooked case of selection bias. The strong agreement between pasture-level models and producer perceptions (Figure 5B and 5D) offers a window into the scale at which producers conceptualize risk and points to potential opportunities for targeted management interventions at fine scales. Our different methods highlight diverse drivers of risk, which suggests that ecologically-driven models and producer perceptions complement one another. Finally, our examination of different risk classification systems for our models offers further insight into the risk perceptions of producers and provides guidance for connecting social and ecological data on predation risk.

The most striking contrast among the different approaches to quantifying risk of livestock predation was between the predation risk model, which classified much of our study site as low risk, and the summary risk perception map, which revealed that producers consider most of the site as high risk (Figure 5A). While previous research has taken such discrepancies to indicate misunderstandings in the perceptions of producers (Gillingham & Lee 2003; Suryawanshi et al. 2013), we propose a different interpretation of the results at this study site. Producer familiarity with the geography and ecology of the study site appears to be high, as evidenced by the accuracy of their mapping of carcass locations in data forms at the study site. Additionally, questionnaire answers reflect producers' understanding of the underlying drivers of their own risk perceptions, and these answers map well onto their intuitive drawings of risk perceptions (Figures 5C and 5D). This consistency suggests that producers are familiar enough with the site and its ecology to make accurate causal links between perceived drivers of risk and its patterning in space. We find it unlikely that producers with such site familiarity would misidentify the patterns of risk as severely as the contrast between the predation risk model and the risk perception maps might suggest.

Therefore, we instead suggest that this contrast highlights an important form of selection bias that is often overlooked in livestock predation research. Risk perceptions are an important driver of producer decisions (Marchini & Macdonald 2012; Scasta et al. 2017; Moreira-Arce et al. 2018). Producers at our site avoided grazing livestock in pastures they perceived to be high risk, and grazed almost all the sites they perceived to be low or medium risk (Figure 3). Almost half of the study site was excluded from grazing due to predation concerns, including the largest pastures, which producers associated with high risk. These producer decisions about husbandry, which are powerfully driven by their risk perceptions, thus have a strong effect on where livestock predation can occur. The data that we used to build our predation risk model were thus already exposed to selection bias by these perception-driven producer decisions. This kind of selection bias has been identified in the ecology of predation risk (Moll et al. 2017) and explored more deeply in other fields (Hernán et al. 2004), but it requires greater attention in the field of livestock-predator conflict. This selection bias likely affects many study systems, especially those, like this study site, where animals are pastured, producers have freedom to use or avoid areas they deem risky, and where models like ours extrapolate findings to areas that producers have chosen to avoid.

Due to this selection bias, we believe inherent patterns of risk at the study site are best identified through a combination of producer risk perceptions and the predation risk model. In areas that producers have already selected against, producer risk perceptions are likely the most accurate reflections of inherent landscape risk. However, within pastures that producers have chosen to graze, predation risk models can make an important contribution to understanding risk, especially at fine spatial scales. Many producers chose to draw their risk perception maps by identifying risk for entire pastures (Figure 3). When we applied each pasture's highest value from the predation risk model to the entire pasture, there was strong agreement between this model and risk perceptions (Figure 5B). This agreement suggests that producers may subscribe to a similar process in evaluating risk, taking a pasture's riskiest elements and applying them to the whole. Interestingly, this line of thinking creates opportunities for targeted, fine-scale management interventions. Within grazed pastures, the predation risk model does not suffer from the selection bias described above, and can thus offer a fine-scale, sub-pasture window into patterns of predation risk. Identifying hotspots of risk within pastures may identify new management opportunities that would not emerge from a pasture-level management viewpoint. For example, the predation risk model identified a network of steep ravines in a pasture as high risk (Figure 2, inset blowup), representing one of the few areas where the predation risk model assigned a higher risk score than that of the risk perception map (Figure 5A). A site like this represents a strong candidate for targeted management and further research, such as through temporary fencing to cordon this potentially high-risk area (Macon et al. 2018).

In addition to mapping spatial patterns of risk, we also identified environmental correlates of risk and risk perceptions. Here too, contrasts between risk perceptions and our predation risk model reveal opportunities for complementary socio-ecological insights. In the predation risk model, habitat variables explained the bulk of variation in likelihood of coyote predation on sheep (Table 1 and Supplementary Table 2). Model results suggest that coyotes may use the cover of locally rugged terrain, dense surrounding chaparral, and neighboring properties with less aggressive predator management to initiate attacks on sheep. Strong associations between predation risk and vernal pools and water sources suggest that these features may concentrate livestock prey, especially in spring when the pools are fullest and

lambs are most vulnerable. While canids are typically considered coursing predators, several of the variables of our predation risk model suggest that coyotes may locally adopt ambush predation strategies when landscape features are amenable to this hunting approach (Sacks & Neale 2002; Preisser et al. 2007b). Interestingly, previous research has shown important connections between drought and conflict (Saberwal et al. 1994; O'Loughlin et al. 2012), and given that our study took place during one of the worst droughts in California history (Griffin & Anchukaitis 2014), the unusually dry conditions could be mediating this behavioral adaptation by concentrating livestock prey.

In contrast to the spatial risk map, which highlighted habitat variables associated with risk, producers considered husbandry factors as central determinants of risk, as shown in both the questionnaire answers and linear regression of the summary perception map (Table 1). During interviews, producers typically discussed habitat in the light of husbandry practices, rather than as meaningful in isolation. For example, producers stated that ruggedness and habitat mattered to the extent that they limited or facilitated guardian dog movements and sightlines for both sheep and producers. In contrast to the predation risk model, producers described coyotes as a coursing predator, susceptible to chase by dogs and reliant on grassland habitats and large pastures to successfully carry out attacks. The predation risk model thus points to specific sites and strategies for testing new management strategies for coyotes as an ambush predator, especially during severe drought conditions. For example, producers might place additional guardian dogs or non-lethal deterrents at vernal pools and along property boundaries where coyotes appear to concentrate attacks. Beyond these specific recommendations, the predation risk model highlights predator adaptability, which, as other studies have shown, necessitates dynamic, adaptive management to mitigate conflict (Stone et al. 2017; Wilson et al. 2017; van Eeden et al. 2018).

One of the strongest points of disagreement between livestock producer perceptions and the predation risk model was the importance of guardian dogs. Producers repeatedly emphasized the importance of guardian dogs during interviews, and both questionnaire answers and the linear regression of the summary perception map further reflected their importance to producer risk perceptions. These perceptions are well founded by research, which has demonstrated the effectiveness of guardian dogs in reducing livestock predation (Green et al. 1984; Coppinger & Coppinger 1988; Andelt 1992; Gehring et al. 2010; van Bommel & Johnson 2012). The predation risk model did not retain guardian dogs as a predictor of risk, however, and it had only a very weak effect in intermediate models before its exclusion. This omission may mask its importance, and shed light on the difficulty of understanding livestock-predator conflict without input from producers. While our model takes the landscape as a static snapshot of a 10-year period, producers dynamically respond to conditions over the course of the year. They commonly deploy more guardian dogs in pastures that they perceive to be riskiest. If the producers are correct about both the high inherent risk of these pastures and the effectiveness of the dogs, then these countervailing effects may be in part responsible for masking the dogs from the predation risk model. Examples of the complexity of mapping risk are common in ecological studies (Moll et al. 2017; Gaynor et al. 2019), but deserve greater attention in the field of livestock-predator conflict. Here, understanding producer perceptions and their associated husbandry decisions reveals not only factors that models may omit, but also reveals a more dynamic landscape that is difficult to capture in a static model. We suggest that future risk mapping exercises account for ongoing management practices and interpret model results in consultation with producers.

Increasing exchange between disciplines when undertaking socio-ecological questions is an important goal for supporting future research and management of livestock predation (Dickman 2010). We adopted multiple methodological approaches that we expected to facilitate easy and meaningful exchange between social and ecological data. To this end, we asked producers to conceptualize risk in equal intervals of low, medium, and high, and we classified our predation risk model and questionnaire data accordingly. However, we found that questionnaire data matched perception maps much better when we used a geometric interval (Figure 5C), which sets much lower thresholds for high risk. Our predation risk model also displayed greater agreement with perception maps when we used a geometric interval (Figure 5A), and we believe this is well supported by the psychology of risk perceptions. Risk perception and tolerance are difficult to internally quantify and are extremely context dependent (Starr 1969). Risk perceptions of wildlife in particular are easily inflated by feelings of vulnerability and lack of control, which typify livestock production (Naughton-Treves & Treves 2005; Skogen et al. 2008; Carter et al. 2012). We recommend that ecologically-driven risk models explore and potentially adopt geometric interval or other similar classifications of risk data to account for low risk tolerances and heightened perceptions of livestock predation risk among producers.

CONCLUSION

In this study, we address several important gaps in the science of livestock-predator conflict and develop a series of complementary methods for considering conflict as a socio-ecological process. Our comparisons of socio-ecological data demonstrate an important but unreported form of selection bias and stress the importance of incorporating producer perceptions and decisions to avoid inaccurate inferences resulting from this bias. Combining producer perceptions and model data has untapped promise for improving understandings of livestock predation risk. Such a combination should consider using producer perceptions in locations that producers deem too risky to graze livestock, while making targeted management interventions at fine scales based on predation risk model outputs. Additionally, predation risk models can reveal underlying ecological dynamics – in this case the identification of coyotes adapting an ambush predation strategy – that may then inform specific management responses. However, other important drivers of risk – in this case the presence of guardian dogs – may be masked in empirical models by dynamic husbandry practices on a complex ecological landscape. We offer a guideline for quantifying risk perceptions that better reflects the psychology of risk perceptions and promotes interoperability between social and ecological data. Involving livestock producers in the science of predator-livestock conflict from start to finish has great promise to produce the most accurate and actionable understandings of conflict and to build trust that will support both wildlife and human livelihoods.

TABLE 1. SPATIAL VARIABLES FOR THREE MODELS OF LIVESTOCK PREDATION RISK.
We compared spatial variables associated with livestock predation risk across three models. Values for the Predation risk model and Linear regression of the summary participatory map show estimates from these two regressions. Values for the Mean questionnaire score show the mean of respondent answers on a 1-5 scale regarding the importance of each variable to livestock predation from not important (1) to critically important (5). Blank boxes indicate that variables were not retained in model selection.

Variable	Predation risk model	Linear regression of participatory map	Mean questionnaire score (1-5)
Habitat			
Chaparral area within 120 m	0.40		3.50
Proportion of chaparral in a pasture			4.00
Vernal pool area within 120 m	0.26		1.13
Woodland area within 120 m			2.63
Grassland area within 120 m		-0.23	2.63
Proportion of grassland in a pasture			4.00
NDVI	-0.48		2.50
Distance to water (squared)	-0.33		2.00
Distance to habitat patch edge	0.27		1.38
Topography			
Ruggedness (500 m window)	-0.95		3.63
Ruggedness (30 m window)	0.74	0.79	3.71
Pasture characteristics			
Pasture size		2.47	3.67
Perimeter to Area ratio of pasture			2.38
Human presence and husbandry			
Height of nearest fence	-0.54		3.38
Condition of nearest fence			3.75
Distance to bedding sites			3.38
Distance to site boundary (squared)	-0.35		1.13
Avg. number of guardian dogs		-0.58	4.75
Distance to BLM property			3.13

FIGURE 1. The study took place at the Hopland Research and Extension Center (HREC), in northern California. This figure illustrates pasture boundaries, grazing areas, and major habitat types within the study site.

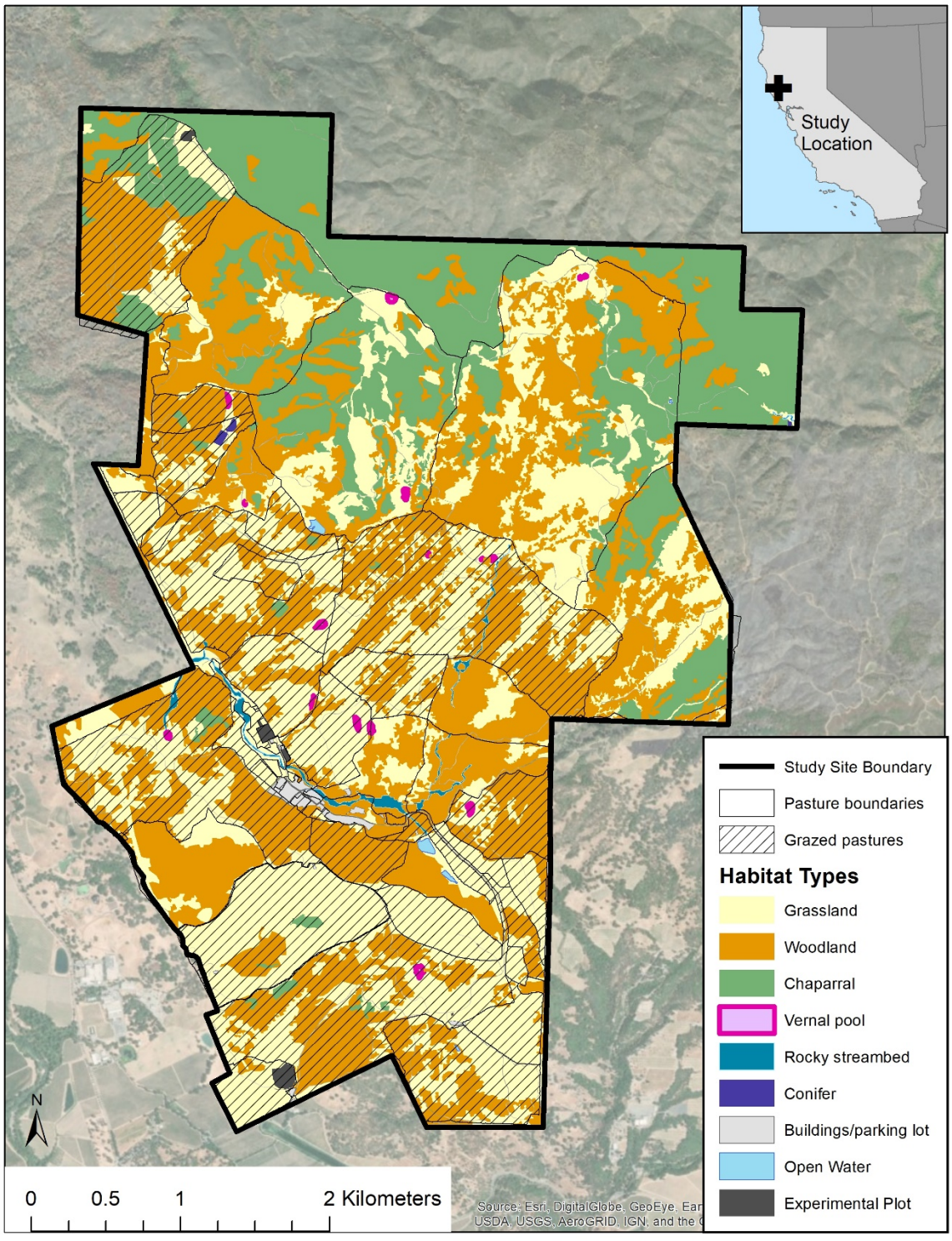


FIGURE 2. Spatial variation in likelihood of coyote predation on sheep, as predicted by the top predation risk model, classified into three categories using A) an equal interval and B) a geometric interval. While we asked producers to score risk according to an equal interval classification, the geometric interval appears to better replicate low risk tolerances and high sensitivities in increases in risk experienced by producers. Inset blowup maps, framed in blue, highlight areas of high predicted risk, according to the predation risk model.

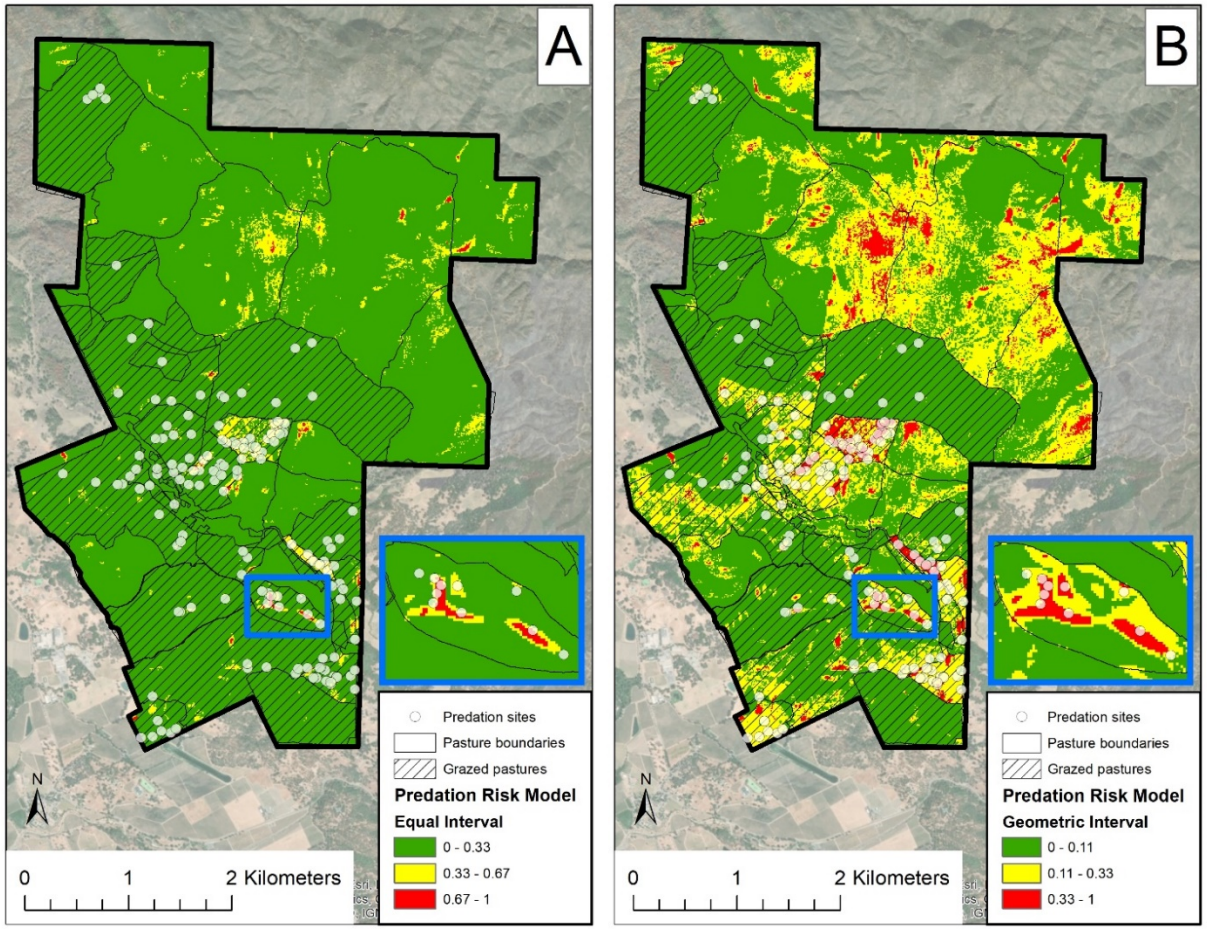


FIGURE 3. Summarized risk perception map, depicting the spatial variation in likelihood of coyote predation on sheep, as perceived by livestock producers. We took mean scores of individual maps in which we asked producers at the study site to draw the risk of livestock predation in equal categories of low (1), medium (2), and high (3) risk at the study site.

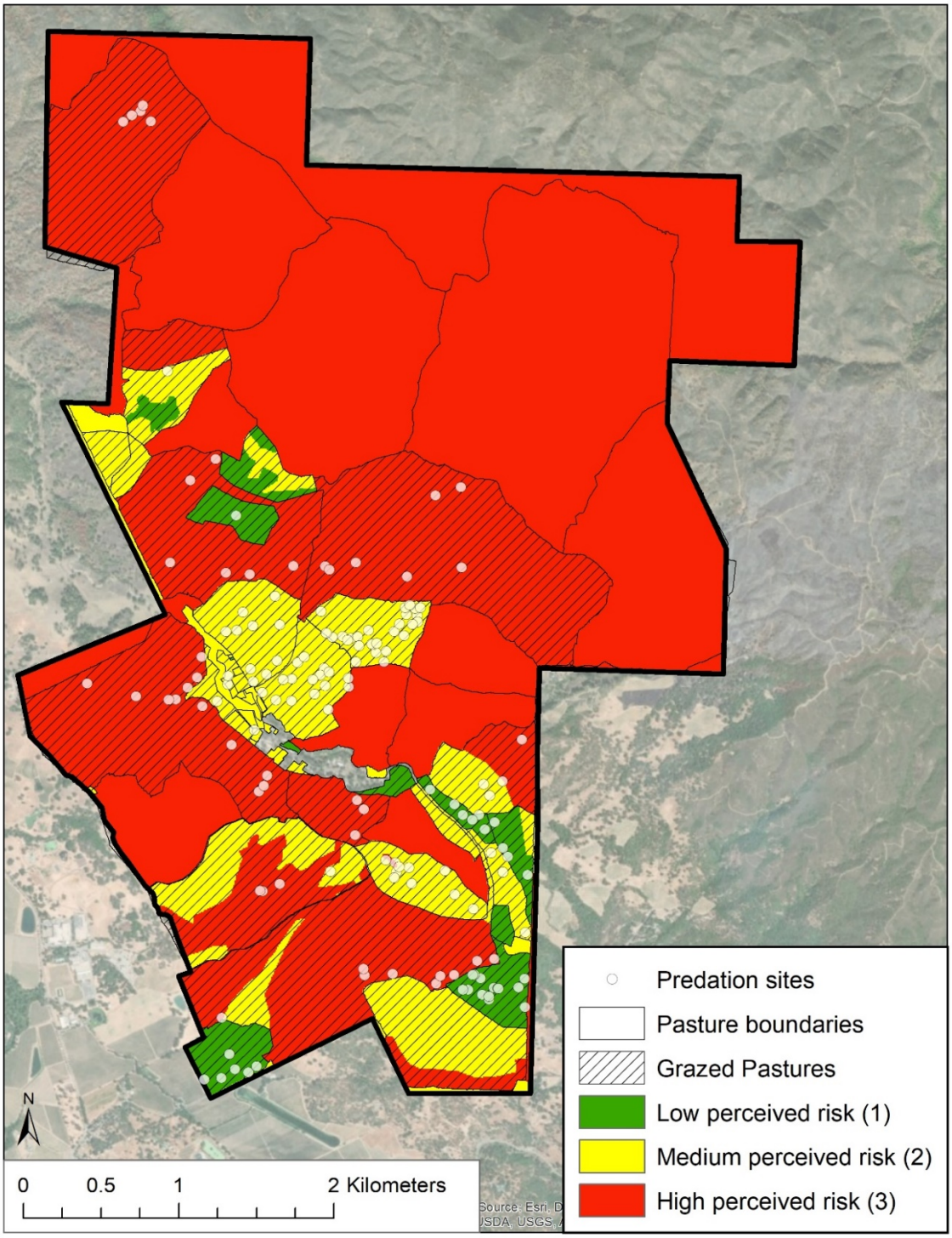


FIGURE 4. Spatial variation in likelihood of coyote predation on sheep, modeled based on factors that livestock producers associated with risk. We used mean questionnaire scores regarding the importance of environmental variables in driving risk to weight spatial layers and produce summary maps. A) 10 m resolution map using a geometric interval to reclassify results. B) Pasture-level map using a geometric interval to reclassify results.

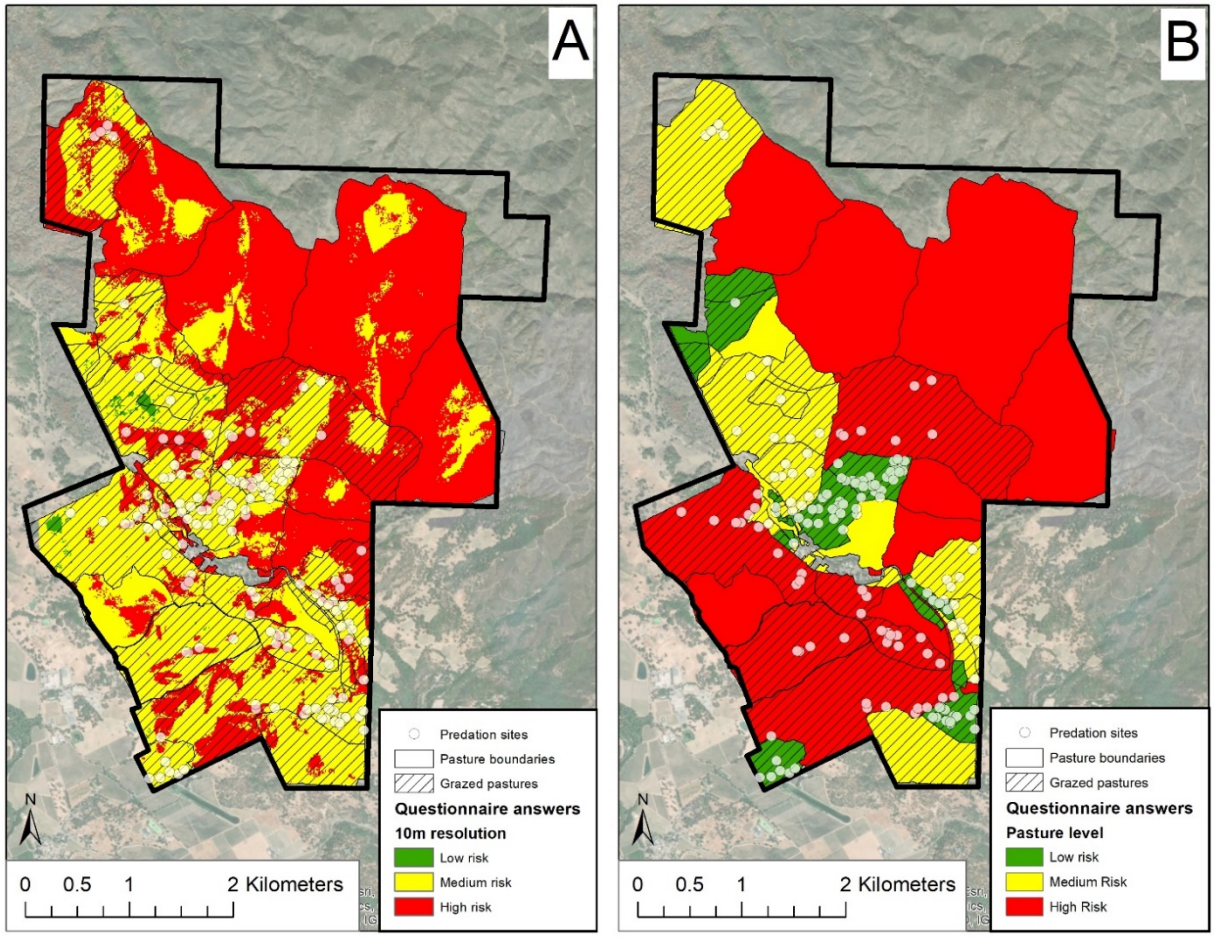
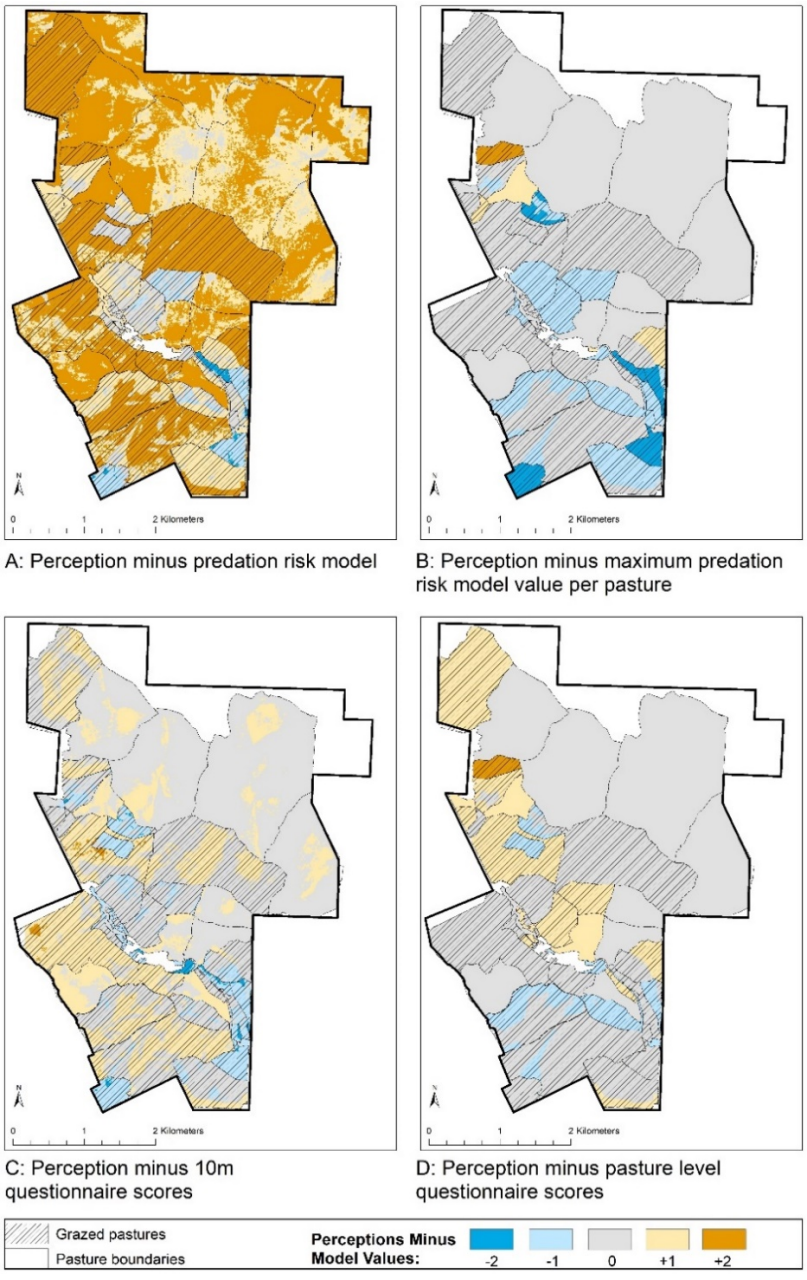


FIGURE 5. Differences in spatial patterns of risk between the summary perception map and other analyses presented in this study. Scores of 0 indicate no difference. Scores of +2 indicate areas of high disagreement, where risk perceptions are high but comparing maps show low risk. Scores of -2 also indicate areas of high disagreement, but they depict areas where risk perceptions are low and comparing maps show high risk. A) Risk perceptions minus our predation risk model reclassified using a geometric interval. B) Risk perception minus our risk perception model, where the highest model value in each pasture was applied to the entire pasture. C) Risk perception minus questionnaire scores mapped at 10 m resolution and reclassified using a geometric interval. D) Risk perception minus questionnaire scores mapped at the pasture level and reclassified using a geometric interval.



SUPPLEMENTARY TABLE 1. VARIABLES RETAINED BY THE TOP-RANKED PREDATION RISK MODEL AFTER MODEL SELECTION.

Variable	Estimate	Standard error	Z-value	p-value
Intercept	-1.830	0.350	-5.226	<0.001
Height of nearest fence	-0.539	0.208	-2.598	0.009
Distance to boundary squared	-0.346	0.190	-1.823	0.068
Ruggedness (30m window)	0.740	0.158	4.675	<0.001
Ruggedness (500m window)	-0.948	0.261	-3.636	<0.001
Distance to water squared	-0.330	0.154	-2.140	0.032
Distance to patch edge	0.275	0.136	2.018	0.044
NDVI	-0.484	0.153	-3.175	0.002
Chaparral within 120m	0.396	0.178	2.229	0.026
Vernal pools within 120m	0.258	0.097	2.665	0.008

SUPPLEMENTARY TABLE 2. VARIABLES INCLUDED IN A DATABASE USED FOR PREDATION RISK MODELING AND LINEAR REGRESSION OF THE SUMMARIZED PARTICIPATORY MAP.
All GIS data was provided by the Hopland Research and Extension Center (HREC). The authors created habitat type data from aerial basemaps provided by HREC, and ground-truthed 50 random control points to ensure accuracy. Coyote relative activity index was calculated using a grid of 36 camera traps deployed at the study site by the authors. For ungrazed pastures, we assumed the average number of guardian dogs per acre would occur. We also assumed that the average number of sheep-nights per acre would occur in these ungrazed pastures. We discussed both of these assumptions with producers at the study site, and they supported these choices.

Variable	Category	Hypothesized Effect on predation risk	Resolution
Chaparral area within 120m	Habitat	Positive. We expect greater risk where closed habitats like chaparral occur	10m
Conifer area within 120m	Habitat	Positive. We expect greater risk where closed habitats like conifers occur	10m
Coyote relative activity index	Habitat	Positive. We expect greater risk where coyote activity is higher.	10m
Distance to habitat patch edge	Habitat	Negative. We expect coyotes to initiate attacks from closed vegetation types, with increasing frequency near borders	10m
Distance to water	Habitat	Negative. We expect water features to concentrate livestock prey, and also to occur in steeper terrain where we expect greater risk	10m
Grassland area within 120m	Habitat	Negative. We expect lower risk in open habitats like grassland	10m
Mean habitat patch size in pasture	Habitat	Negative. We expect greater predation risk in pastures with smaller patches, where more covered attack initiation sites occur	pasture vector
Normalized Difference Vegetation Index (NDVI)	Habitat	Positive. We expect greater risk where vegetation is denser	10m
Open water area within 120m	Habitat	Positive. We expect water features to concentrate livestock prey	10m
Rocky stream area within 120m	Habitat	Positive. We expect water features to concentrate livestock prey, and rocky streambeds to limit anti-predator behaviors	10m
Vernal pool area within 120m	Habitat	Positive. We expect water features to concentrate livestock prey	10m
Woodland area within 120m	Habitat	Positive. We expect greater risk where closed habitats like woodland occur	10m
Average sheep-nights per pasture	Human presence and husbandry	NA. We used this as a random effect in our predation risk model.	pasture vector
Barbwire on nearest fence	Human presence and husbandry	Negative. We expect lower risk when additional strands of barb wire are used on fences	10m

Variable	Category	Hypothesized Effect on predation risk	Resolution
Building area within 120m	Human presence and husbandry	Negative. We expect lower risk where human activity is more frequent around buildings	10m
Condition of nearest fence	Human presence and husbandry	Negative. We expect fences in better condition to reduce risk	10m
Distance to BLM land	Human presence and husbandry	Negative. We expect more predation near BLM lands where human activity is infrequent	10m
Distance to buildings	Human presence and husbandry	Negative. We expect greater risk further from buildings where human activity is less frequent	10m
Distance to headquarters	Human presence and husbandry	Negative. We expect greater risk further from headquarters where human activity is less frequent	10m
Distance to nearest fence	Human presence and husbandry	Negative. We predict coyotes to initiate attacks from neighboring pastures without guardian dogs, and opportunistically attack sheep near fences	10m
Distance to road	Human presence and husbandry	Negative. We expect greater risk further from roads, where human activity is less frequent	10m
Distance to site boundary	Human presence and husbandry	Positive. We expect greater risk near the site boundary, where predator management strategies are less common	10m
Experimental plot area within 120m	Human presence and husbandry	Negative. We expect lower risk where human activity is more frequent around experimental plots	10m
Guardian dogs per acre	Human presence and husbandry	Negative. We expect lower risk where more guardian dogs occur	pasture vector
Height of nearest fence	Human presence and husbandry	Negative. We predict coyotes to be deterred by higher fences that are more difficult to jump	10m
Pasture average guardian dogs	Human presence and husbandry	Negative. We expect lower risk where more guardian dogs occur	pasture vector
Type of nearest fence	Human presence and husbandry	Variable. We expect electric fences to most effectively reduce risk, followed by woven wire fences, followed by single strand	10m
Pasture perimeter-to-area ratio	Pasture characteristics	Positive. We expect greater predation risk where more attack initiation sites per area from neighboring pastures are available	pasture vector
Pasture size	Pasture characteristics	Positive. We expect greater risk in large pastures where husbandry practices to limit predation are more difficult	pasture vector
Elevation	Topography	Positive. We expect greater risk at higher elevations where habitat is more closed and human activity infrequent	10m
Pasture max ruggedness (1200m window)	Topography	Positive. We expect greater risk in rugged terrain, where anti-predator behaviors and flight are more difficult	pasture vector

Variable	Category	Hypothesized Effect on predation risk	Resolution
Pasture max ruggedness (30m window)	Topography	Positive. We expect greater risk in rugged terrain, where anti-predator behaviors and flight are more difficult	pasture vector
Pasture mean ruggedness (1200m window)	Topography	Positive. We expect greater risk in rugged terrain, where anti-predator behaviors and flight are more difficult	pasture vector
Pasture mean ruggedness (30m window)	Topography	Positive. We expect greater risk in rugged terrain, where anti-predator behaviors and flight are more difficult	pasture vector
Ruggedness – 1200m window	Topography	Positive. We expect greater risk in rugged terrain, where anti-predator behaviors and flight are more difficult	10m
Ruggedness – 250m window	Topography	Positive. We expect greater risk in rugged terrain, where anti-predator behaviors and flight are more difficult	10m
Ruggedness – 30m window	Topography	Positive. We expect greater risk in rugged terrain, where anti-predator behaviors and flight are more difficult	10m
Ruggedness – 500m window	Topography	Positive. We expect greater risk in rugged terrain, where anti-predator behaviors and flight are more difficult	10m
Ruggedness – 800m window	Topography	Positive. We expect greater risk in rugged terrain, where anti-predator behaviors and flight are more difficult	10m
Slope	Topography	Positive. We expect greater risk on steeper slopes where anti-predator behaviors and flight are more difficult	10m

SUPPLEMENTARY FIGURE 1. We conducted participatory mapping with livestock producers to understand their risk perceptions as they varied over space. We asked producers to color a basemap in equal intervals of low, medium, and high risk of predation after we conducted an unstructured interview. Pictured here is the participatory mapping in progress. We have edited this image for the anonymity of human subjects.

Chapter 4. Holes in the fence: The ecological effects of fencing are widespread but poorly understood

ABSTRACT

The last two decades of research in conservation biology have established critical links between the physical and spatial characteristics of human infrastructure and effects on a range of ecological phenomena. Studies of the effects of roads in particular have been substantial enough to form a prolific subdiscipline of "road ecology." Fences are similarly ubiquitous with established ecological impacts, yet they have not been the targets of synoptic research efforts and are often omitted from global discussions of anthropogenic impacts on the environment. Here we provide a systematic review of the literature on fencing and some of the first analyses on the large-scale extent of its impacts. We present five major takeaways from this analysis: 1) We provide a clear definition of fencing to frame methods and a conceptual underpinning for a "fence ecology;" 2) We show that fences have been overlooked in part because they are difficult to map, and so we map a conservative estimate of fencing at over 1 million km for the rural western United States; 3) Through our literature review, we show that the consequences of fences are not exclusively positive or negative but rather reorganize systems and species into "winners and losers;" 4) We show that fences can exert these impacts on every scale of ecological analysis, and we provide a typology of their effects across scales to guide future research; 5) While there is a sufficient body of research to make these first four points, we show that trends and biases in existing research likely mean that the global effects of fences have been greatly underestimated, and many effects likely remain to be discovered.

INTRODUCTION

Fences are one of the most widespread manmade features on Earth, and they may outstretch roads by an order of magnitude (Jakes et al. 2018). While recent popular attention on border fences has made headlines – Europe, for example, now has more kilometers of border fencing than it did during the cold war (Vallet 2016) – these barriers represent a tiny fraction of a rapidly spreading global network of fences. Unlike roads and other forms of linear infrastructure, there exists no formal synthesis of the fences that encircle our planet. Recent case studies have charted the local explosion of fencing and the dangerous social and ecological collapses that can follow (Hoole & Berkes 2010; Løvschal et al. 2017). Studies like these have prompted calls for focused investigations into the potentially devastating and undiscovered consequences of fencing for ecosystems and for new frameworks to guide research and management (Sutherland et al. 2013; Jakes et al. 2018).

Calls for research into the ecological impacts of fences, however, are set against their long history as a tool for managing and even protecting wildlife and habitat. In New Zealand and Australia, fences have famously provided lines of defense against harmful invasive species (Moseby & Read 2006). In Africa, dozens of publications have made the case both for and against fencing for conservation (Hayward et al. 2007; Packer et al. 2013; Creel et al. 2013a; Woodroffe et al. 2014; Durant et al. 2015), while in North America and Europe, authors have proposed innovative forms of fencing with the goal of reducing wildlife-vehicle collisions (Clevenger et al. 2001; Klar et al. 2009). Throughout the world, land managers and restoration

ecologists have successfully employed fences to protect and rehabilitate fragile habitats, especially from the impacts of livestock and invasive species (Spooner et al. 2002; Denmead et al. 2015). Fences thus have the ability to both benefit and harm the ecosystems in which they occur, making the absence of systematic studies of their ecological effects all the more glaring.

There are reasons, however, that fences have eluded systematic study for so long. Fences are both difficult to detect, and, at an even more basic level, difficult to define. Fencing has become a popular metaphor in many disciplines from ecology to computing. Even within ecological studies of fencing, there is considerable semantic drift in what constitutes a fence, as we discuss further below. Where fences have been sufficiently defined, unlike many other forms of infrastructure, they can elude detection, even using sophisticated imagery-driven methods that underpin many global change assessments (Poor et al. 2014). As a result, fences are often framed as a management tool rather than a globally significant ecological feature, and they are a notable omission from efforts to map global infrastructure, including the human footprint (Sanderson et al. 2002). The great variation in composition, structure and function of fences further complicates efforts to summarize their effects. Taken together, these factors may explain how we find ourselves with few general lessons or even broad approaches to understanding the ecological consequences of one of the most ubiquitous features of human civilization on our planet.

As fences finally begin to gain recognition for their potentially enormous effects on ecosystems, there is a need to establish the underpinnings of a fence ecology that can identify fences, locate them spatially, unpack their striking or nuanced impacts, and direct research. Here we lay out a series of frameworks to help identify the breadth of fence effects, place them in context, and define needs and gaps for future research. We offer five major takeaways from the discussions presented below. First, we present an operational definition of fencing to maintain focus on the most widespread and impactful features meriting discussion. We discuss the important variation in type and scale of fences even within this definition, as well as the significance of construction and deterioration of fences over time. Second, we comment on the difficulties in mapping fences and their impacts, which have likely delayed meaningful large-scale science (Box 1). We provide one of the first large-scale estimates of fence density in the Western US to demonstrate how this feature might modify well-established spatial estimates of human impacts (Leu et al. 2008). Third, we show that the consequences of the diverse effects of fences are not strictly beneficial or harmful and instead vary widely by species, system, and context. We offer a guide to commonly described “winners and losers” in a fenced world. Fourth, we present a typology of the potential impacts at every scale of ecological analysis and show that a large body of idiosyncratic literature on fences has demonstrated diverse effects (Gadd 2011). We propose this typology as an organizing framework to help prioritize future research. Fifth, we present perhaps the most important finding of this analysis, in which we describe the trends and biases present in the existing literature on fences. We show that a large body of literature has revealed surprisingly little about the potential consequences of fences, and that a predictive and comprehensive “fence ecology” demands further research to address these shortfalls.

WHAT IS A FENCE?

Narrowing the conversation

A recent publication by Jakes et al. (2018) defined *fence ecology* as "the interactions between fences, wildlife, ecosystems, and societal needs." While we would expand this definition to include all organisms beyond just "wildlife" – which connotes species of value to humans – we believe it offers a succinct and useful summation of what fence ecology might come to include. However, to facilitate the development of fence ecology into a subdiscipline of its own in the mold of road ecology, a clear and concise definition of what constitutes a fence is needed. Fence metaphors are deployed widely across a range of fields, and so our first restriction on the definition is to discuss only physical fences occurring on the terrestrial landscape. Even with this restriction in place, the diversity of tools and approaches that go by the name "fence," as well as those qualifying features that go by other names, make this task more difficult than it seems. How, for example, does a fence differ from a wall, and are such differences ecologically significant? Should innovative tactics in the realm of human-wildlife conflict, such as bee, chili pepper, or sonic "fences," be considered fences? If "fence" represents everything from a 10-meter wall separating nations to the strategic placement of beehives, can we realistically draw conclusions about their effects? We believe the answer to this question is no, and that a narrower definition is required.

There is, as yet, no unifying definition of fences, but for the purposes of this discussion, we defined fences to allow for consistency and clarity while considering the distinct ecological impacts of the vast majority of fences worldwide. We define a fence as *a physical linear structure on the landscape with vertical structural components and non-continuous structures between these vertical components* (Figure 1). Fences are thus differentially permeable to species and processes, and may be quickly constructed and deconstructed by people. This definition excludes walls, for example, which are typified by completely solid features rather than intermittent components, and thus may impose a different set of effects due to their opacity and permeability compared to fences. Bee, chili, and sonic fences, mentioned above, are characterized by non-linear shapes and do not feature physical structural components, and thus also do not fit our definition. Neither do hedgerows or other intentional uses of vegetation to structure landscapes. While some ecological effects of these non-fence barriers may resemble the effects of fences as defined here, others will differ markedly, as will the mechanisms underlying their effects. For this reason, we will abide by the specific definition of a fence mentioned above, a description that allows a common lens to examine the vast majority of ecological impacts of fences throughout the world.

Temporal dynamics of fencing

Fencing, as we define it here, is much more dynamic than many kinds of linear infrastructure. Compared to many other types of infrastructure, fences are much faster to construct, and fence proliferation is occurring rapidly at borders around the world (Linnell et al. 2016). Construction of new fences also frequently accompanies shifting systems of land tenure (Li et al. 2006; Evans & Adams n.d.). In many areas of the world, especially developing areas, privatization and subdivision of land is increasingly common (Yan & Wu 2005). Fences are a primary tool in manifesting and enforcing these changing policies (Yeh 2005; Richard et al. 2006; Said et al. 2016). As with many ecological phenomena, the pace of change is an essential consideration for

understanding its impacts, and it is no different with fences. Recent documentation of extreme rates of fence growth in Africa, for example, hint that the pace of change has thwarted the ability of species and systems to adapt, resulting in local ecosystem collapse (Løvschal et al. 2017).

While fences may be established rapidly, they can also deteriorate quickly, which adds to their dynamic nature on the landscape and the difficulty in quantifying their extent. The level of maintenance or decay of a fence is essential to its effectiveness at its intended purpose and may drastically change its ecological effects (Pirie et al. 2017). Keeping fences "tight" was long a central occupation of pastoralists, but now other fence builders have come to understand its importance. Conservationists, for example, have found that invasive species rapidly discover and exploit breaks in fences (Connolly et al. 2009), undercutting their purpose when regular maintenance is not possible (McKnight 1969; Dube et al. 2010; Scofield et al. 2011; Kesch et al. 2014). Thus, even where fences can be mapped, either remotely or via ground surveys, characterizing their intactness or functionality requires a closer, and often infeasible, form of evaluation.

While we can define fences suitably to support the development of a fence ecology, the variation in physical characteristics, spatial distribution, and construction and decay over time result in widely variable effects of fences. This variation alone points to the need for both guiding frameworks and context-specific research to determine the consequences of a fenced world. Below we define a typology of fence impacts for fences as defined here to help manage this complexity.

ARE FENCES DESTROYING ECOSYSTEMS OR PROTECTING THEM?

The question of whether fences are beneficial or harmful to the systems in which they occur has raged for more than a decade (Hayward & Kerley 2009; Packer et al. 2013; Creel et al. 2013a; Woodroffe et al. 2014; Durant et al. 2015) and can now be more readily answered with a clear definition of what makes a fence. We conducted a systematic literature review to better understand the diverse impacts of fences and whether they help or harm the systems in which they occur (Supplementary methods).

Unsurprisingly, the answer to this question is nuanced. Fences can neither unequivocally protect or harm ecosystems. The effects of fences on their ecological surroundings are diverse, and the same fence can be both beneficial or detrimental depending on species, scale, and type of effect considered. For example, several studies have shown that conservation fences in Africa may protect vulnerable wildlife species from poaching and other human impacts, but, if aligned unfavorably, they may also prohibit the same species from accessing essential resources like watering holes (Ferguson & Hanks 2010). Given this, we suggest that fence ecology should consider not just the blatantly deleterious consequences of fences, but rather take a broader view that fences reorganize the species and systems in which they occur. To put it simply, in a fenced world, there are winners and there are losers (Table 1).

In the sections below, we describe general trends that typify the ecological winners and losers of a fenced world. We define winners as species or systems for which the conditions supporting long-term survival and functioning improve; losers conversely are species or systems facing impediments to survival and functioning due to fences. We discuss trends by species first, but note that the focus on species-level effects of fences is a major bias, to which we will return later in this paper. We also discuss traits and systems that tend to become winners or losers,

according to our review of the literature. This section demonstrates that even where fences are erected for beneficial purposes, such as conservation or restoration, the scales and contexts in which they also create losers is an essential but often overlooked outcome of fence construction.

Fence purposes and their outcomes

Major patterns typifying winners and losers emerged from our review, as summarized in Table 1. One of the most notable patterns, which deserves greater research, is that many fences create winners and losers based on the intentions of the fence builders (Supplementary Table 1). In other words, when fences are built for a specific species or purpose, they often achieve that purpose. Conservation and restoration fences, for example, have great support within the literature for their beneficial effects on wildlife and sensitive plant species for which they are built, making such species "winners" in the fencing game. There is a critical lack of information on species that are not the targets for which fences are built, as our review has shown that only 10.7% of studies focus on non-target species (Supplementary Table 2). For example, a fence in south-eastern Australia, while effectively preventing the ingress of target pest species to an enclosed nature reserve, was found to have unintended negative consequences for native reptil populations around the enclosure, especially for eastern long-necked turtles (*Chelodina longicollis*). The fence disrupted turtle movement patterns, isolated populations, and led to high mortality rates at the fence where turtles were entangled, demonstrating one cost of "successful" fences on non-target species (Ferronato et al. 2014). Further research is needed on the effects of fences on non-target species, but it is likely that many non-targets will experience impacts from fences.

Other examples point to the entanglement of fences and management when it comes to target species. One study unpacked this complexity by examining a case study where a fence was removed between adjacent nature reserves in South Africa. While this fence removal was initially proclaimed a success by enlarging the protected area and increasing connectivity for wildlife, there were differential outcomes for different species. After fence removal, management focused on the "Big 5" wildlife species originally found only in the larger of the two reserves. As a result, obligate grazer species like sable (*Hippotragus niger*), roan (*Hippotragus equinus*), tsessebe (*Damaliscus lunatus*) and eland (*Taurotragus oryx*) that had been thriving in the smaller fenced reserve declined in spite of fence removal, as a new management regime favored more charismatic species (Child 2010). As this study demonstrates, often the clearest winners due to fencing are the species that humans care most about. Thus, management of fenced areas, like fences themselves, may often successfully support targeted species, and, once again, further research is required to better understand how non-targets fare in a fenced world.

Species-level predictors

Some species navigate fences successfully regardless of their stature as a target of fences or management. In particular, as with many kinds of disturbance and infrastructure, generalists and disturbance specialists become winners in a fenced world. Fences may restrict access, change the community composition, or otherwise alter the ecology of systems on which specialist species depend. At a larger scale, specialized systems, those with sensitive dependence on component species or species interactions, are also more likely to experience state shifts due to fencing according to trends found in this review. Conversely, generalist species, and especially disturbance specialists, may readily adapt to the multiple scales of impacts that fences create. For

example, multiple studies point to bird species already adapted to roadside areas or agricultural systems, like the Red-winged blackbird (*Agelaius phoeniceus*), Loggerhead shrike (*Lanius ludovicianus migrans*), or Great tit (*Parus major*), readily incorporating fences into their habitats (Camp & Best 1994; Lesiński 2000; Eseley & Bollinger 2001). Invasive species often are those that also readily adapt to novel or disturbed habitats. Thus, while many fences targeted toward the prevention of the spread of invasive species have a demonstrated record of success, other kinds of fences facilitate invasive species (Conway & Nordstrom 2003; Brown et al. 2006; Loo et al. 2009). In a particularly ironic case in Australia, fences, a favored tool for limiting invasive species in this country, facilitated invasive Cane toads (*Bufo marinus*) which moved preferentially along cleared fencelines. Comparatively little research has been conducted on this topic, and it deserves much greater research attention.

In addition to their ability to adapt to disturbance or rapid ecosystem change, other traits of species help determine their sensitivity to the effects of fences. Highly mobile animals, for example, are more likely to encounter fences and become exposed to their dangers, even in areas where fences may otherwise be providing benefits. An abundance of research has focused on large ungulates, as discussed further below, and the disastrous effects of fences on migratory ungulates, such as the loss of blue wildebeest (*Connochaetes taurinus*) migration in Africa, was some of the earliest research to point to the ecological losers of a fenced world (Owens & Owens 1984). Even when migratory species are not blocked by fences, their ability and willingness to cross these features still has important effects on their habitat selection and resource access. African elephants (*Loxodonta africana*), for example, avoid crossable fences and subsequently alter their environments via their effects as ecosystem engineers (Vanak et al. 2010).

Avifauna also demonstrate the importance of species' traits in their sensitivity to fences. While many species may readily ignore fences or even incorporate them into their habitat selection, ground nesting birds, like members of the grouse genus (*Tetrao*), may have high mortality rates due to fences, especially where fences blend in with background habitat features (Catt et al. 1994; Baines & Andrew 2003). Many reptile species also appear to have a special sensitivity, especially to electric fences, due to the prolonged physical contact they may experience in crawling over or under fences, as opposed to flying, leaping, or digging beneath them (Ferronato et al. 2014).

Winners and losers at larger scales

As noted above, it is important to point out the species-level bias in considering the impacts of fences: research in our review usually identified winners one species at a time. There are many fewer examples of whole communities or ecosystems as winners resulting from fences. Even where conservation or restoration enclose large habitats, research still points to differential outcomes for constituent species. Within conservation fences for example, mobile species with larger range sizes may in fact fare worse inside reserves than outside of them due to the restricting effects of fences (Imbahale et al. 2008; Cole et al. 2012; Creel et al. 2013a). Pathogens and parasites may spread more rapidly where species interactions are concentrated within reserves. For example, smaller fenced reserves predicted higher rates of gastrointestinal parasite infection rates among impala (*Aepyceros melampus*) in central Kenya (Ezenwa 2004). For fences around roads, research has almost exclusively been conducted to test effectiveness of fences in creating winners; losers may exist at multiple scales, but defining a whole ecosystem-level outcome in such cases is difficult. However, many studies demonstrated the ways in which

fences accompanying livestock management or subdivision of land altered nutrient flows, redistributed wildlife species and altered plant compositions, leading to habitat state shifts toward lower diversity and fewer native species. Recent studies have identified the potential for ecosystem collapse when fence densities are high enough, as processes across all ecological scales are affected.

Difficult tradeoffs are inherent in a fenced world, which creates winners and losers at different scales. In many cases, fences may be an almost inevitable accompaniment to many forms of infrastructure and economic livelihoods. However, the trend of proliferation of fencing suggests the potential for a dangerous future in which fences simultaneously and rapidly alter ecological processes at multiple scales, likely producing more losers than winners, and potentially resulting in ecosystem state shift or collapse (Løvschal et al. 2017). In light of this, we do not advocate for a general policy with respect to fences. Instead, we suggest to scientists that additional research on fencing is required, especially for non-target species, complex large-scale effects, and the potential for multi-scale fence effects to trigger irreversible consequences. For managers, we suggest considering the construction or removal of fences not merely with specific target species in mind, but with a broader consideration of the manifold effects fences may have at multiple scales.

MOVING FORWARD: A TYPOLOGY OF FENCE IMPACTS TO GUIDE RESEARCH

Our review uncovered evidence for the effects of fences at every ecological scale, from the physiology and behavioral decisions of individual organisms to the functioning of entire ecosystems (Table 2). However, our review also showed that research on fences has typically focused on a single scale at a time, and often on a single species at a time. This means that the existing body of literature on fences, in spite of being large in number of studies, is idiosyncratic, narrowly focused, and as yet fails to provide suitable frameworks or guidelines for research. We provide a typology of impact types categorized by ecological scale and 34 specific effect types as one framework for guiding future research (Table 2; Supplementary methods).

An essential component of future empirical work on fencing will be linking effects across scales. The accumulation of ecological effects at multiple spatial scales means fences can have potentially dire consequences. While we note that fences can produce winners and not just losers, dense networks of fences can initiate ecosystem collapse due to the multiple scales of effects they have, an increasingly pressing concern as fences rapidly proliferate throughout the world (Løvschal et al. 2017). While we have divided our typology by ecological scale, it is important to reiterate that the linkages across scales are a critical need for research.

Physiological and behavioral effects of fences

At the smallest scales, the primary effects of fencing are physiological or behavioral. A robust literature on movement and crossing behaviors shows the physiological and fitness risks that fences can impose as animals search for breaks (Connolly et al. 2009), alter their optimal movement or foraging patterns (Vanak et al. 2010), and adopt crossing behaviors or are injured or killed in efforts to cross (Harrington & Conover 2006; Gates et al. 2011). Several studies have shown that mobile species constantly patrol fence boundaries seeking breaks and finding them within hours. In New Zealand's Maungatautari Ecological Island, a heavily fenced reserve that

excludes invasive mammals, rats (*Rattus rattus*) and other small mammals constantly patrolled the fence and typically identified fence breaks within 24 hours (Connolly et al. 2009).

While many of these small-scale effects have been documented as directly affecting wildlife, plants and other non-wildlife species are not immune to small-scale effects of fences. Many plant species have been shown to accumulate along fences, especially along larger infrastructure fences like sand and snow fences (Nordstrom et al. 2009; Loik et al. 2013). Indirect effects of fences on plants are also common. For example, domestic and wild herbivores preferentially move and feed alongside fence lines, resulting in increased trampling, changed growth patterns, and altered seed dispersal (Evans 1997; Grudzinski et al. 2016). Cumulatively, such changes can alter recruitment and plant community composition, as exemplified by the semi-arid succulent thicket biome in South Africa, where contrast studies across fencelines reveal changes in composition, litter production, and decomposition (Lechmere-Oertel et al. 2008). Restricting animal movements may also have important protective effects for plants and range-restricted species, with numerous studies showing the restorative effects fences provide when they prevent trampling or herbivory, especially of sensitive riparian habitats (Opperman & Merenlender 2000; Loo et al. 2009; Muller et al. 2016).

Population effects of fences

The cumulative effects of physiological and behavioral changes accumulate at larger scales to affect whole populations. For wildlife species, studies have shown fences alter movement and habitat selection patterns that alter population distributions (Chirima et al. 2012). When migrations are critical to species survival, several high-profile studies have shown the catastrophic effects of impermeable fences that cross migration routes and the resulting population declines that follow, especially for wildebeest migrations in southern Africa (Owens & Owens 1984; Whyte & Joubert 1988). Similarly, where fences impede connectivity, genetic isolation or reduced gene flow may occur. A striking example showed that a planned US-Mexico border fence would dangerously restrict gene flow among desert bighorn sheep (*Ovis canadensis mexicana*), isolating populations across the border (Flesch et al. 2010). Demographic changes may also be detected if phenotypic differences result in differential mortality or distribution within populations. Interestingly, for very small-bodied species, fences may constitute landscape features that create habitat. Several studies show birds and insects using fences as nesting, lookout, feeding, or display sites (e.g., Lesinski 2000), but further research is needed to understand the ways in which fences produce microhabitat variation.

Community effects of fences

At larger scales, fences may have effects on species interactions and community composition, either directly or through the snowballing of smaller-scale changes. One study clearly showed the potential of fences to alter community composition, demonstrating that African wild dogs (*Lycaon pictus*) in Botswana readily crossed a fence to find spatial refuge from competing lions (*Panthera leo*), which showed a reluctance to cross the fence's narrowly spaced wires (Cozzi et al. 2013). Several studies made clear that even when fences do not so strictly partition species, they can still radically modify the strength of species interactions. For example, predator and prey behavior and distributions, altered by fences, may scale up to influence the outcome of this interaction. Altered interactions like these also may facilitate or inhibit the success of invasive species. While fences by reputation have been used to prevent the spread of such species, several

papers also identified their role in enabling the establishment of invasive species (Brown et al. 2006; Weller et al. 2011). In Australia, for example, restoration fences excluding livestock sped the invasion of the exotic aquatic grass *Glyceria maxima* (Loo et al. 2009).

Ecosystem effects of fences

The combination of the effects of fences mentioned here, as well as numerous others identified in our review, can markedly alter entire ecosystems. At the ecosystem scale, however, it is difficult and unrealistic to view fences in total isolation. In Australia, some of the world's longest fences have been paired with eradications of large predators like dingoes (*Canis lupus dingo*) to protect livestock grazing areas. While these enormous fences will have behavioral, population, and community level effects, some of their most important consequences are apparent as changes to entire ecosystems. Without dingoes, researchers have tracked a continental-scale mesopredator release that has altered biodiversity and habitats over enormous areas of Australia (Letnic et al. 2011). As this example highlights, fences are important but overlooked components of many of the world's most powerful engines of change: livestock grazing, privatization and subdivision of land, road development, human settlement, and even conservation. The cumulative effects at multiple ecological scales of a global network of fences only adds to the effects of these other drivers of ecosystem change. A number of "fence-line contrast" studies show just how severe this change can be when fences enforce differential management (Todd & Hoffman 1999; Lechmere-Oertel et al. 2008; McGahey 2010).

We do not wish to argue that all fences are detrimental to species and communities. Individual fences may serve powerful conservation or restoration functions and, in many cases, merit the high regard in which they are held as a management tool. However, our review makes clear that these roles can also obscure the cumulative, large-scale effects of a globally ubiquitous network of fences. Future research on the ecology of fences must strive to not consider these features in isolation, but to collect empirical data and theorize the multiple scales of impacts which fencing can create.

TRENDS IN FENCE ECOLOGY RESEARCH

Perhaps the most important finding for supporting a new subdiscipline of fence ecology is identifying gaps in research. The large number of studies we reviewed (446) belies a shallow and narrow understanding of the global impacts of fences. The strong topical and geographical biases found in the published literature on fences mean that what is left to learn about fences far surpasses what is already known. It is likely that these trends reflect the identities, interests, and goals of fence researchers and not the proportional geographical and topical distribution of fence effects, and we discuss these trends in this light.

We call attention to five important sources of bias that characterize the literature on fences: 1) a taxonomic bias, meaning that fence research, has focused on economically important game species, especially medium-sized ungulates; 2) a scale bias, meaning that fence research has paid disproportionately little attention to complex community and ecosystem-level processes; 3) a geographic bias, meaning that fence research has primarily come from a few countries found in temperate regions with large rangelands; 4) biases in the type of fence studied, meaning that much of our inference about the fences that stretch furthest (e.g., livestock fences) must be drawn from those that may be built quite differently (e.g., conservation fences); and 5) biases in the

relationship between study species and fence purpose, meaning that we know little about species for which fences were not designed.

1) Taxonomic biases

Large mammal species have received by far the most research attention of any taxon. More than half of the studies in our review considered mammals as their focal species (Table 3). Within mammals, ungulates were the most common subcategory, with 124 of the 446 studies focused exclusively on ungulates approximately 100 kg in mass, the largest such focal group within the studies reviewed. Taken together with the abundance of research on movement and distribution of species, these results suggest that much of the research on fencing has demonstrated that fences that effectively control livestock movements and distributions have similar effects on large mammalian wildlife species. This is not entirely surprising, considering the economic importance of such species as game animals and their phenological similarity to livestock species for which many fences have been built. Nevertheless, the range of fence studies we examined suggests a disproportionate emphasis on medium-sized ungulates that may come at a cost to other species whose responses to fence-induced changes deserves further inquiry.

The effects of fences on these mammals' movements and distributions has received the most consideration from research in fence ecology (Table 2). Some of the earliest studies that we reviewed considered how fences that were built to restrict the movements of domestic ungulates might have similar effects on wild ungulate movements (Spencer 1948; Bauer 1964; Tierson 1969; Messner & Dietz 1973). This question has continued to preoccupy research on fencing, as some of the most cited (Owens & Owens 1984; Whyte & Joubert 1988; Mbaiwa & Mbaiwa 2006) and most recent studies (Jakes et al. 2018) that we reviewed have focused on effects of fences on wildlife movements.

In short, a large quantity of our knowledge about the ecological effects of fences tells us that fences restrict the movement and distributions of medium-sized ungulates.

2) Scale biases

While research has uncovered a great deal about large ungulates, complex ecological processes altered by fences have received far less research attention. The large number of studies showing ecosystem effects in Table 2 masks the overlap in these research efforts: most of these point to systemic recoveries in small plots when livestock are fenced out. Many important large-scale findings remain understudied. Some of the least studied topics in our review include hydrological effects, facilitation or inhibition of invasive species, changes in diseases susceptibility, changes in demography or carrying capacity, and alteration of social behaviors (Table 2). These ecological processes are far removed from the purposes for which most fences have been built. Similarly, only 37 of the 446 studies considered multiple focal species. The studies that did incorporate multiple focal taxa support several decades of research in community ecology by indicating that single species effects can cascade to the communities in which they occur, and may even have continental-scale effects (Letnic et al. 2011). There are likely numerous impact types of fences yet to be discovered as a result of the scarce research on complex processes.

3) Geographical biases

Our review showed startling trends in the geographical distribution of studies (Figure 3). Within the 446 studies we reviewed, research has been concentrated in only a few nations, with five

countries (United States, Australia, South Africa, China, and Botswana) accounting for over 50% of the studies reviewed here (Supplementary Table 3). The United States was the site of 93 of the reviewed studies, accounting for over 20% of the total volume of reviewed studies. North America (121 studies) and Africa (106 studies) were the most studied continents, while South America (15) was the least. The tropics, where much of the world's biodiversity occurs and where some of the most rapid proliferation in the types of land uses typically accompanied by fences is taking place, are particularly depauperate in fence research (Figure 3). It is likely that they host important and diverse fence impacts that are underreported or as yet undiscovered.

Major research themes dominate each continent, meaning that the topical knowledge available on fences often comes only from a particular geographic context (Figure 4). For example, most of the fence research in Africa has focused on conservation fencing, and conversely, much of our knowledge on conservation fencing comes from Africa. The same is true for invasive species fences in Australia, and livestock fencing in Asia, although there is much research on livestock fencing from other continents as well. Infrastructure fencing, primarily focused around roads, comes almost entirely from North America and Europe. Diversifying both the topics and the geography in which fence research occurs is thus a pressing need. Even more importantly, it is clear that vast parts of the world, including much of South America, have had no research conducted on the ecological effects of fencing (Figure 3), meaning that many context-specific consequences of fencing likely remain to be discovered.

4) Biases in fence types studied

Important trends also occur in the type of fences that have been studied, and we categorized fences according to the purpose of their construction (Supplementary Table 1). Conservation fencing has been the subject of greatest study, and has received disproportionate attention for its total length relative to other fences. While livestock fencing has been the subject of the second largest number of studies, it is likely the most common fence type throughout the world, and thus has proportionately few studies relative to its total length. Each of these fence types is distinct, and drawing conclusions across types is thus problematic. The effects of a tall, electrified conservation fence cannot fairly be applied to a short, single-strand livestock fence.

Livestock fences in particular merit much greater research given their ubiquity throughout the world. Compared to most other fence types, livestock fences are much more permeable to many species. We also classified the permeability of fences to the study species, and our results show that impermeable fences were the most well-studied, accounting for 40% of included studies, while semi-permeable (23%) and fully permeable (19%) were considered less frequently. Interesting research has begun to characterize the effects of permeable fences on species, but much greater research is needed to go beyond the simple conclusion that fences restrict species for which they are impermeable.

5) Biases in research targets

Here we offer a simple but dramatic finding, that 64% of studies focused exclusively on the effects of fencing on target species, that is, species for which a fence was built. Only 24% of studies included both target and non-target species and a mere 12% studied non-targets exclusively. Some of the most profound effects of fencing happen to non-target species and systems (Ferronato et al. 2014), even as research focuses heavily on testing whether fences have effects on the species for which they were built. This is perhaps the most glaring omission in all

of fence research, and shows that research often reflects the intentions and needs of fence builders. There is likely a frightening diversity of impacts to non-target species that remain unreported.

CONCLUSION

Fence ecology exists, but it is in its infancy. The impressive quantity of research on the effects of fencing, taken together, still tells us little about the overall breadth of fence impacts. What is clear from this research, however, is that fences have a surprising potential to exert influence on every scale of ecology. Their effects range across taxa, and include mobile and sessile species, large and small species, as well as whole communities and ecosystems. Future research on the ecology of fences is desperately needed. Here we have provided a definition and series of frameworks, guidance, and questions to help focus future research. We encourage researchers to think outside of the box, to stretch their questions across scales, and to include those species and systems which fences may not have been built to affect. We especially encourage researchers from continents and biomes that have conducted little fence research to contribute to our broader understanding. Understanding the winners and losers of a fenced world is more important every day, as fences rapidly proliferate and densify. We hope that a robust fence ecology grows even more rapidly to give us the knowledge and capacity to mitigate these effects.

BOX 1. INVISIBLE FENCES, INVISIBLE IMPACTS

Fences are a globally ubiquitous feature. They have accompanied human settlements for millennia (Kotchemidova 2008), but they also occur in remote, unsettled areas to delineate boundaries or cordon livestock. Unlike roads, which modern cartographic and remote sensing technologies can typically detect (Mnih & Hinton 2010), most of the world's fences remain uncharted, and we found no large-scale and few small-scale efforts to map fences. Where recent research has attempted remote sensing of fences, evidence suggests that fences may outstrip roads substantially (Poor et al. 2014; Jakes et al. 2018). Furthermore, as fencing materials have become cheaper and more widely available, their use is accelerating. For example, the practice of fencing roads is increasingly common, both to mitigate wildlife-vehicle strikes, but also to manage snow drifts, and has now become standard practice in many countries (Peaden et al. 2017). The rapid increase in fencing further highlights the importance of understanding their effects on nature.

While it may be difficult to map the dynamic global network of fences, it is possible to make meaningful estimates about fence densities where data is available. We estimated the length of fencing and fence densities in the western United States using a very conservative model to predict the presence of fences. We followed methods and assumptions developed by Poor (2014), but implemented these methods at a larger scale. At this scale, we could not expect to identify all private property boundaries without acquiring costly parcel data. However, most boundaries at the regional scale are defined by or against the boundaries in federal lands. Within federal lands, grazing makes up the primary land use, and we acquired data on federal pasture boundaries with federal property boundaries to determine rural grazing fence distribution. We also assumed primary and secondary roads would be fenced, and included these in our analysis. We did not attempt to model fence densities in urban or suburban areas, where other types of infrastructure and land use would likely complicate or outweigh the impacts of fences. We estimated over 1 million km of fences in the western US, without including urban and suburban property fences.

We calculated a kernel density surrounding these fence approximations at a distance of 50km, which was greater than the largest distance from any given site in the region to its nearest fence (Figure 2A). As expected, this model shows high densities of fencing around urban areas, with lower densities characterizing most rural and remote parts of the western U.S. However, several areas stood out as having high densities of fencing despite their remoteness from human settlements. We compared this fence density map to the human footprint in the western United States(Leu et al. 2008) and highlighted regions where fence densities are high, but the human footprint is low (Figure 2B). Several areas of high fence density and low estimated human footprint reiterate the point that the extent of ecological impacts of fences on species and systems have likely yet to be captured by models and approaches attempting to understand global change.

BOX 2. FENCES AND PEOPLE

So far, we have spent comparatively little time discussing the effects of fences on humans, human communities, and economies. Indeed, to do justice to this topic would require a separate treatment entirely. However, to our surprise, over 70 studies in our review considered the effects of fences on humans (Table 2), and so we include a brief discussion of our findings here for context.

Certainly, there are ways in which fences directly affect humans – border fences famously exemplify this throughout the world, though in many cases they are as effective at altering local ecology as the human movements for which they were designed (McCallum et al. 2014; Linnell et al. 2016). Conservation fences have also had an important and controversial role in limiting human movement and access to natural areas (Spierenburg & Wels 2006; Chaminuka 2010). In some cases, fences have prompted strong local opposition, as they have not only excluded communities from access to important natural resources, but also decoupled people from their lands, traditions, and stories (Hoole & Berkes 2010). Such human effects must also be incorporated into the science and management of fencing to avoid conflict. In one successful example, local communities along the controversial Makgadikgadi fence in Botswana have been given the right to request re-alignment, mitigating human conflicts without conservation losses (Brooks & Bradley 2010).

While fences can directly affect humans, they more commonly create indirect effects for people. Livestock fences provide many examples of the varied indirect effects of fences on humans. A clear trend in recent papers is the use of fences to enforce increasing privatization of land and sedentarization of landholders. Fences clearly demarcate boundaries and may help achieve political aims (Xu et al. 2015; Evans & Adams n.d.). The effects of privatization on ecology have been mixed, though in some areas research has shown that higher stocking rates and reduced mobility of pastoralists accompanying fencing and privatization have degraded grassland productivity and diversity (Li 2007). For people, the hard, private boundaries established by fences not only interrupt traditional life ways based on communal grazing areas, but may also impact economic livelihoods by restricting access to important grazing areas and resources. These same fences may also engender conflict among humans when pasture conditions and resources vary across fencelines (Mbaiwa 2008, Cao 2011). In an example from Kenya, a fence proposed to prevent human-elephant conflict was aligned, constructed, and maintained in accordance with political aims and with little input from affected pastoralists. Smallholders were forced to graze new lands, while large private landholders could increase stocking rates and exclude trespassers (Evans & Adams n.d.). A clear trend seems that the winners in cases like this are large private or state landowners with entrenched power (Albertson 2010; Knight & Cowling 2012; Hongslo 2015; Evans & Adams n.d.).

Importantly, these human effects are not distinct from environmental ones. Sedentarization, overstocking of rangelands, and disempowerment of local inhabitants routinely leads to further environmental change and degradation. A clear symbol of this kind of feedback is found when communities deprived of resource access by conservation fences use fence materials to construct snares that have devastating impacts for wildlife the fences were meant to protect (Dunham 2001; Lindsey et al. 2011). Pastoralists in newly fenced land must alter communal grazing patterns and increase stocking rates and resource use to ensure their livelihood, resulting in range degradation. Environmental degradation, restricted access, and

shifting economic demands that accompany fences may create a feedback loop that causes more intensive use of surrounding environments, resulting in further ecological impacts, and in some cases, impelling people to engage in criminal activities.

At a larger scale, research has shown that fences entrench ecological consequences and limit adaptability. Even where they may have beneficial effects, such as limiting human-wildlife conflict, their permanent placement amplifies other ecological impacts over time on a dynamic landscape, creating long-term consequences for human inhabitants (Taylor & Martin 1987; McGahey 2010). For example, in Malaysia, an initially successful network of fences to limit human-elephant conflict ultimately restricted elephant access to important natural habitats, and ultimately conflict increased, as elephants were forced to raid plantations (Estes et al. 2012). Where privatization, rapidly shifting grazing regimes, and fence development coincide, ecosystem collapses may occur suddenly (Knight & Cowling 2012; Løvschal et al. 2017). Fences are not universally impactful to people, however, and may have many benefits depending on the context. Some research has pointed to the economic gains through ecotourism that fenced reserves have helped create both locally and internationally (Slotow 2012). Even beyond economics, successful conservation or restoration fences may help improve morale and support from surrounding communities for conservation goals (BURNS et al. 2011), or even protect culturally important environmental features for people (Ens et al. 2016). Fencing remains one of the primary tools for limiting human-wildlife conflict, and many studies note its successes in spite of some counterexamples mentioned above (Linhart et al. 1982; O'Connell-Rodwell et al. 2000; Honda & Iijima 2016). Road fences continue to prove effective in limiting wildlife-vehicle collisions, which may prevent not just wildlife mortality, but human mortality as well (LEBLOND et al. 2007). As with the ecological effects of fences mentioned above, fences have complex, scale-dependent, dynamic consequences for people, which must also be given deeper consideration by both scientists and managers alike.

FIGURE 1. Fences require a specific and broadly applicable definition to allow for the establishment of consistent methods and frameworks in fence ecology. Here we define a fence as a physical linear structure on the landscape with vertical structural components and intermittent, non-continuous structures between these vertical components. Examples of structures fitting this definition include A) an electrified elephant fence in Kenya, B) a woven wire livestock fence in California, and C) a dingo fence in Australia. Examples of structures not fitting this definition include D) a border wall between Israel and Palestine, E) a honey bee fence in Kenya, and F) a hedgerow in England.

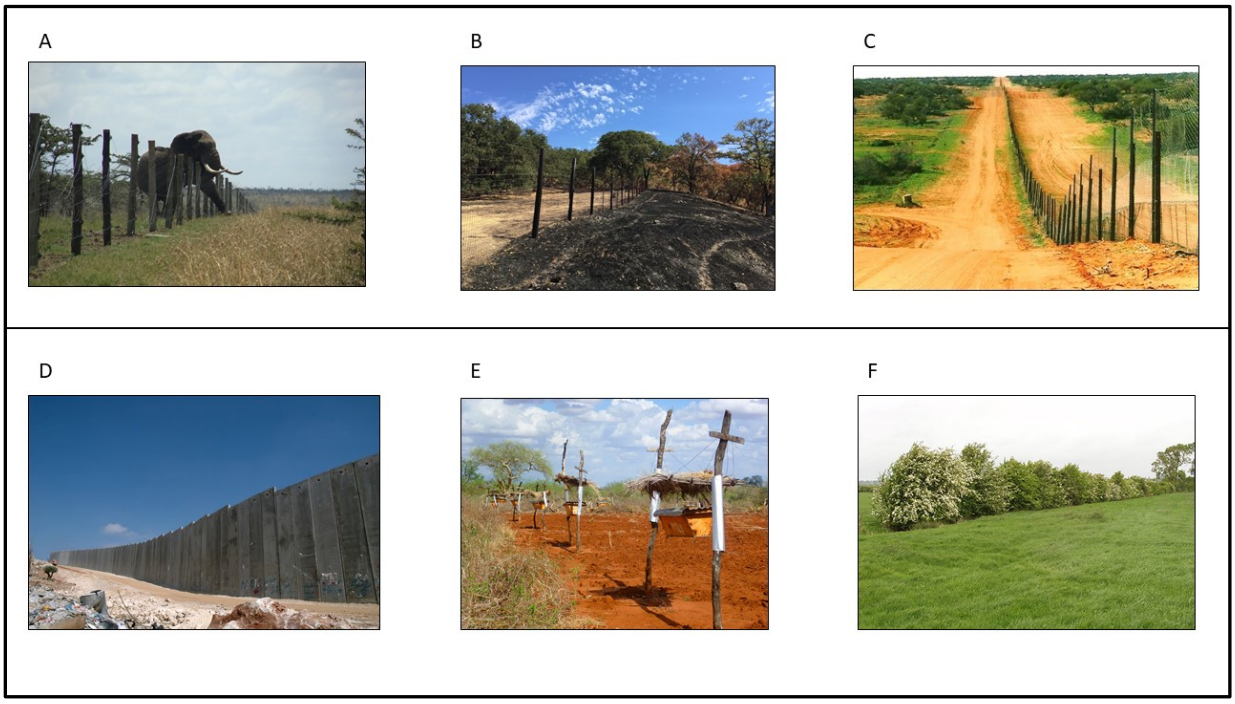


FIGURE 2. We conducted one of the first large-scale analyses of the spatial extent of fencing in the western United States. We assembled a conservative dataset of potential fence lines and A) calculated the nearest distance to any given fence to be less than 50 km, with a mean of 3.1km, and B) identified areas of medium and high fence densities whose human footprint has likely been underestimated.

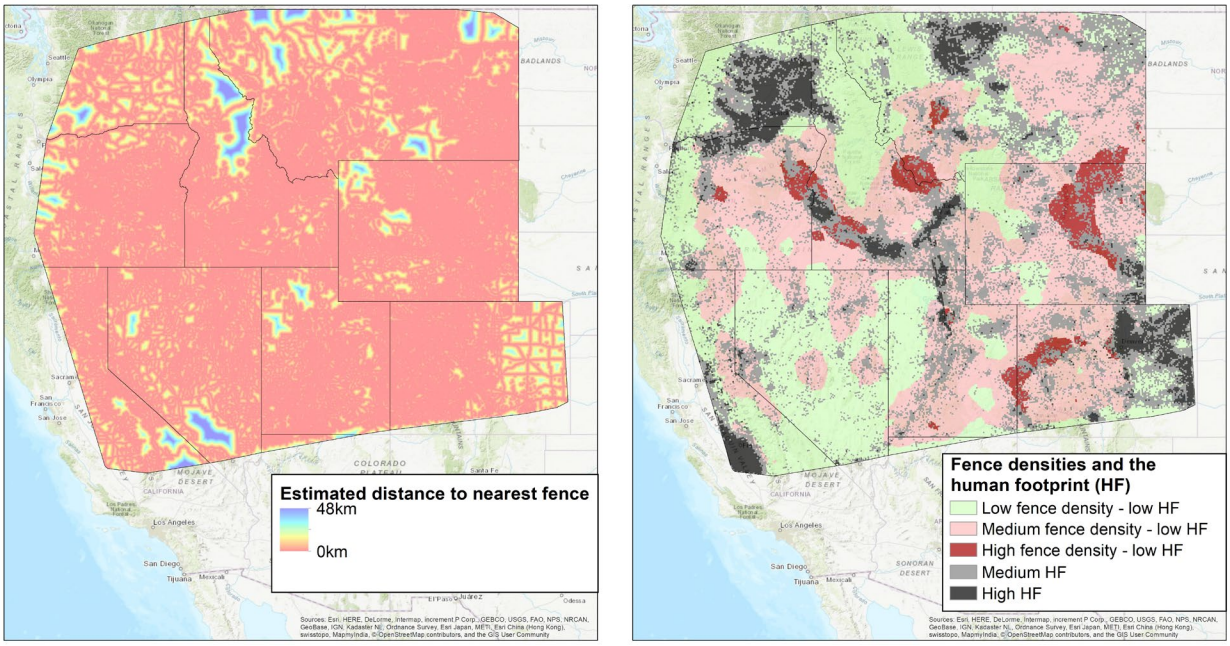


FIGURE 3. Study locations and countries where fence research has been conducted. 60 countries have been home to research on the ecological effects of fences, but 38 of these have had only 1 such study. Five countries account for more than 50% of the studies reviewed here.

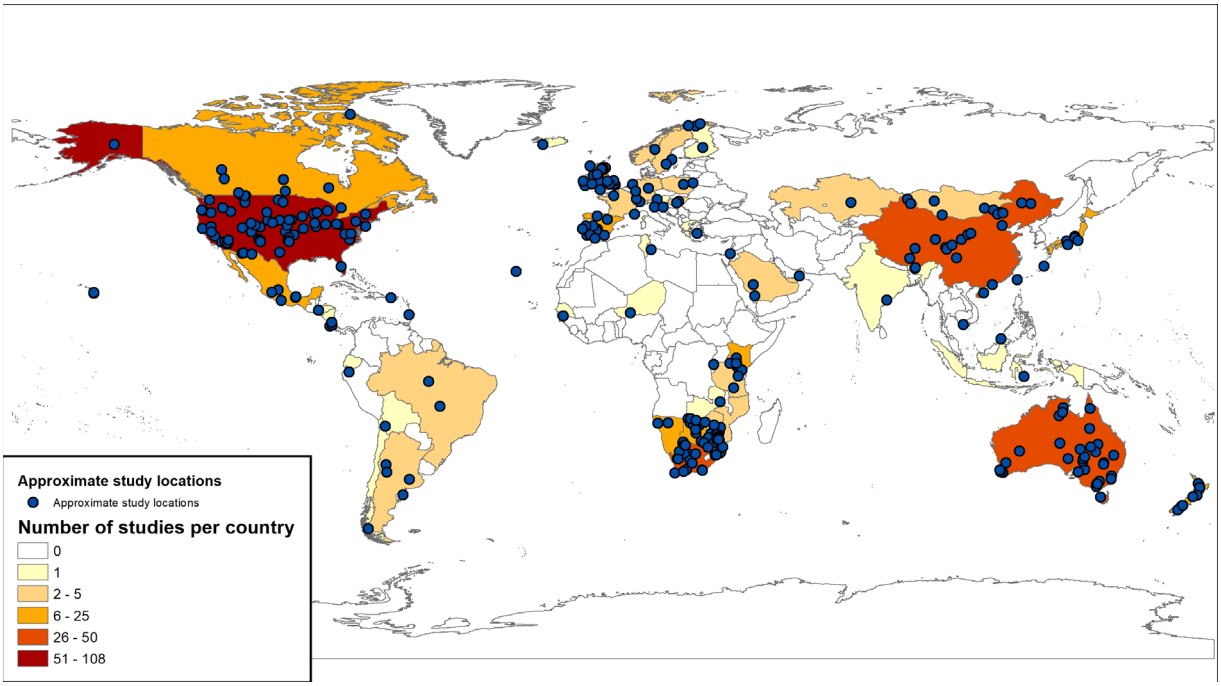


FIGURE 4. The type of fences studied in each continent. Several continents have a clearly dominant focal type of fence within their body of research. Likewise, several fence types have been primarily researched on single continents. Diversity in both the geography of research and the type of research conducted is a clear need for future efforts in fence ecology.

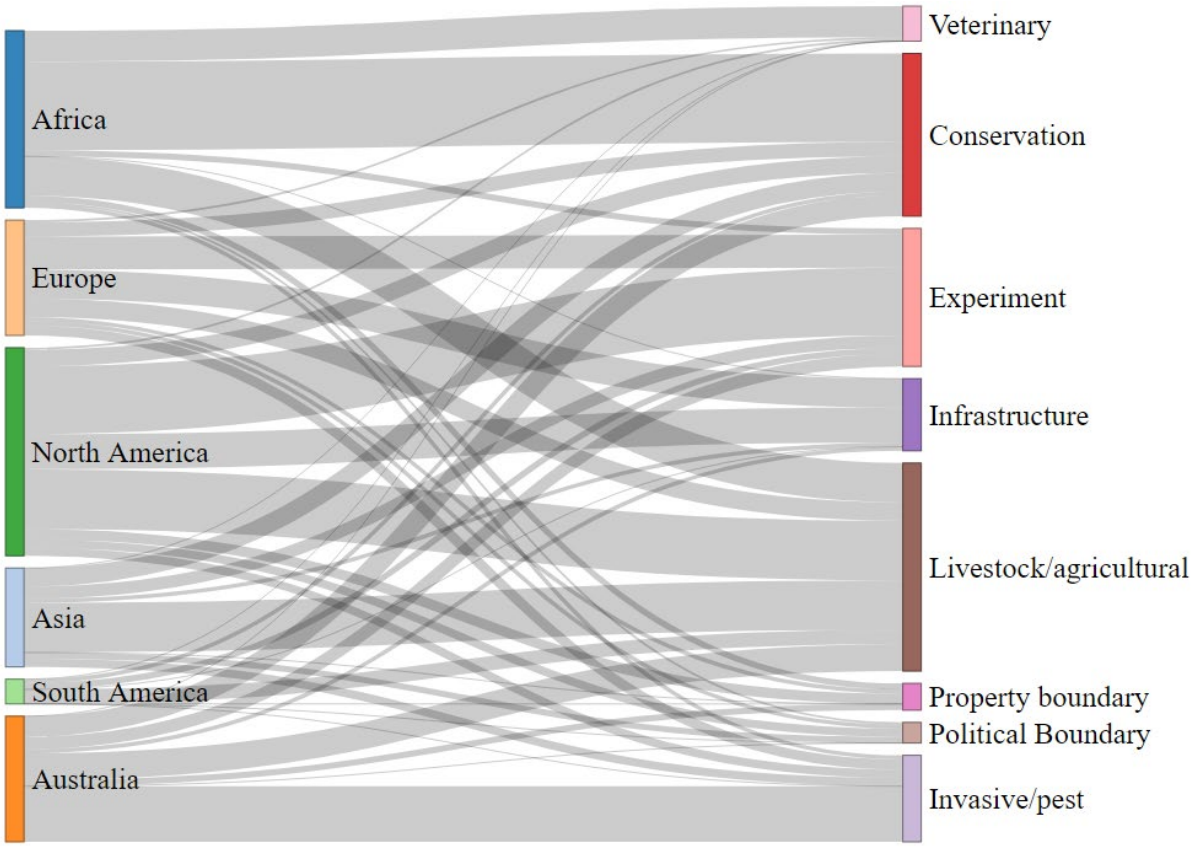


TABLE 1. CHARACTERISTICS OF FENCES, INCLUDING PURPOSE, FEATURES, EXTENT, AND ECOLOGICAL WINNERS AND LOSERS

Fence purpose	Typical Fence Characteristics	Winners	Losers	Extent
Conservation/ Restoration	Closed Expensive construction Impermeable to people/ livestock Impermeable to target species inside Paired with focused management	Sensitive species where human or livestock impacts are likely Species/systems whose biology/phenology allows them to thrive within a closed fence (e.g., smaller ranged species, small self-contained ecosystems) Marketable/charismatic species who benefit from management in a closed system Pathogens and parasites reliant on contact networks Unwanted species difficult to eradicate, which may be released from predation or competition Game species, when protections from fences outweigh their supplying of raw materials for snares	Species outside or inside the fence who are excluded from essential resources Less marketable/ charismatic species that are not management targets Systems/functions that cannot occur within a confined area Species susceptible to disease spread Game species, when the materials provided by fences for snares outweighs their protections	Hotspots worldwide, most commonly studied in Africa
Infrastructure	Open Expensive construction Designed for specific species or guilds Paired with other management tools (e.g., underpasses)	Target species in danger of injury or conflict from infrastructure (e.g., wildlife-vehicle collisions) Disturbance specialists or generalists that can incorporate fences into habitat Invasive species requiring easy movement pathways	Non-target species or systems inhibited by fences but not infrastructure	Widespread along roads and development, especially in North America and Europe

Fence purpose	Typical Fence Characteristics	Winners	Losers	Extent
Livestock/ agricultural	Closed Impermeable to livestock Easy and cheap to construct Paired with range management and grazing	High variation in livestock fence density makes winners and losers highly context dependent Livestock Invasive plants Private landowners Humans and wildlife adversely affected by human-wildlife conflict	High variation in livestock fence density makes winners and losers highly context dependent Native plant biodiversity Vegetation growing along fencelines where trampling is common Soil and plant productivity Migratory terrestrial wildlife Ground nesting birds Smallholders or communal grazers reliant on open range	Extremely common worldwide, extensive in rangelands
Political boundaries	Open Large scale Expensive Well maintained Impermeable to many species	Generalists, disturbance specialists, and invasive species	Large mobile wildlife species, and the systems in which they occur Specialist species Habitats falling across borders Wind propagated plants	Infrequent, at select boundaries only. Large in scale where they occur
Property boundaries	Closed Small scale Low cost Frequently maintained	Generalists, disturbance specialists, and invasive species Species benefitting from human shields Sensitive habitats bordering encroaching developed properties	Large mobile wildlife species; the systems in which they occur Humans reliant on communal or non-demarcated property Wind propagated plants Ground nesting birds	Common in already developed areas, but infrequent elsewhere. Increasingly common as property regimes shift globally

Fence purpose	Typical Fence Characteristics	Winners	Losers	Extent
Invasive/pest	Closed Very large scale Expensive Impermeable to target invasive/pest species Paired with aggressive management (e.g., eradications, frequent maintenance, restoration)	Prey/competitors of excluded species Native species/systems, where invasive species are effectively controlled	Large mobile wildlife species, and the systems in which they occur Livestock predators, when they are the "pests" being managed Biodiversity, when large native predators are controlled	Infrequent, but large-scale where present

TABLE 2. TYPOLOGY OF ECOLOGICAL IMPACTS CAUSED BY FENCES AND THE NUMBER OF STUDIES EXAMINING EACH IMPACT TYPE

Impact	Scale	Study count
Injury or fitness change	physiology	27
Energy expenditure change	physiology	21
	Physiology total	***41***
Movement	behavior	140
Crossing	behavior	123
Foraging	behavior	64
Migration disruption	behavior	36
Predation or evasion strategy	behavior	29
Social behavior	behavior	3
	Behavior total	***207***
Distribution	population	103
Altered population density	population	76
Prevention of mortality	population	70
Direct mortality	population	50
Improved habitat suitability	population	49
Indirect mortality	population	43
Increased recruitment	population	43
Population Isolation Reduced gene flow	population	38
Reduced habitat suitability	population	29
Reduced carrying capacity	population	14
Demography	population	13
	Population total	***258***
Community composition shift	community	92
Species partitioning	community	52
Multi-trophic effects	community	40
Altered interaction strength	community	37
Inhibition of invasive species	community	12
Increased disease susceptibility	community	10
Facilitation of invasive species	community	8
Reduced disease susceptibility	community	7
	Community total	***150***
Ecosystem process alteration	ecosystem	65
Habitat state change	ecosystem	35
Erosion	ecosystem	15
Habitat destruction	ecosystem	13
Hydrological shifts	ecosystem	11
	Ecosystem total	***92***
	Human effects	***107***

TABLE 3. NUMBER OF FENCE STUDIES BY PRIMARY FOCAL TAXON

Taxon	Number of studies	Percent of total studies
Mammals	247	55.4%
Vegetation	71	15.9%
Multiple taxa	37	8.3%
Birds	29	6.5%
Herpetofauna	20	4.5%
Humans	19	4.3%
Invertebrates	16	3.6%
Fungi	2	0.4%
Fish	1	0.2%

SUPPLEMENTARY METHODS

We conducted a systematic literature to better understand the diverse impacts of fences. Using Web of Science, we created a list of studies using the following search terms: “fence ecolog*;” “fence biolog*;” “fence conservation;” “barrier ecolog*;” “barrier biolog*;” “barrier conservation;” “wall ecolog*;” “wall biolog*;” and “wall conservation.” In addition, we snowballed 10 key papers which we identified as critical in the recent development of fence ecology. We created a list of 1401 papers from these search criteria.

Of these 1401 papers, we determined whether each should be included or excluded from our review. Included papers featured discussions of material (rather than figurative or metaphorical fences) and measured ecological effects directly relating to fencing. Studies or reports relying on opinion were excluded from the review. Papers using secondary data were also excluded, unless they drew novel conclusions from these data. However, we also considered the studies providing the source data for review in these cases. We also excluded research that studied exclosure fences designed specifically for the experiment. The reason for excluding these studies is that such fence designs are often temporary, small in scale, highly specific to a given study taxa and therefore not representative of the widespread effects of fencing, and typically focused on the exclusion of a species rather than the effects of a fence itself. However, we included such studies when they tested applied fence designs.

We encountered many special cases of fencing in conducting this review. We defined fences as vertical, manmade structures featuring intermittent structural components supporting intervening materials like wire or pipe. Non-vertical (eg cattleguards), chemical (eg chili pepper fences), and other systems frequently referred to as “fences” did not fit our definition and so were excluded. Live fences were included, but we also analyzed our data with these special fences excluded. Fences may also refer to structural components: sand fences, for example, help establish sand dunes, but may become completely buried. In the latter case, we excluded them from our review, but they were included if the fence itself met our definition, remained above ground, and its ecological effects were studied. The same criteria were applied to snow fences, certain kinds of stream fencing, and other structural fencing.

After applying our exclusion criteria, we reviewed the 446 remaining studies. For each study, we collected a variety of information regarding geography, methods, fence metadata, and ecological effects of fencing. We noted the continent, country, and state in which each study occurred, and produced maps identifying hot and cold spots of fence research. We also examined whether studies used control-treatment designs with and without fences, or whether they made ad hoc observations of the effects of fencing. More specifically, we noted what methods studies used, including empirical data collection, modeling, interviews, and other approaches. When it was provided, we collected detailed information on the fences studied, including height, length, whether they were open or enclosed, the purpose of the fence, its permeability to the study species (impermeable, semi-permeable, or fully permeable), whether vegetation was cleared around the fenceline, the primary materials used in its construction and maintenance, and its construction year. Rarely was all of this information available in a given study.

The bulk of our review process focused on the ecological effects of fencing. We broke down these effects into domains of ecological study, as follows: physiological effects, behavioral effects, population effects, community effects, and ecosystem effects. Within each of these broader domains, we also noted more specific ecological effects of fences, including positive

impacts. While impacts on humans and human communities were diverse, we lumped these into a single "human effects" category. We tallied these data to identify trends and gaps in our current understanding of the effects of fencing on ecology.

In addition to this quantitative data, we also developed more qualitative findings from the papers considered in this review. From these studies, we developed a list of attributes of "winners and losers" in systems that feature fences, as well as the circumstances in which these outcomes occur. Additionally, we considered how the ecological effects of fencing are scale-dependent, and identified relevant spatial scales at which effects occur.

We also categorized studies in this review based on their focal taxa. Broadly, we broke studies down into nine taxonomic groups: birds, fish, herpetofauna, mammals, invertebrates, fungi, plants, and humans. When more than one of these broad taxonomic groups featured in a study, we classified it as "multiple." We subcategorized these taxa into taxonomic orders, and for mammals, further into families. Though the taxonomic organization of ungulates is disputed, we used this designation as one of our mammal subcategories. We also classified study species by body mass, according to their closest order of magnitude in kilograms.

SUPPLEMENTARY TABLE 1. NUMBER OF STUDIES BY DESIGNATED FENCING PURPOSE

Fence Type	Percent of total studies
conservation	18.12%
livestock	17.00%
experiment	15.66%
invasive/pest	9.62%
infrastructure	8.72%
agricultural	6.26%
veterinary	4.25%
property boundary	3.13%
political boundary	2.46%
multiple	0.89%

SUPPLEMENTARY TABLE 2. NUMBER OF STUDIES BY TARGET OR NON-TARGET SPECIES

Target or non-target of fence construction	Percent of total studies
Target	64.6%
Non-target	11.8%
Both	23.6%

SUPPLEMENTARY TABLE 3. COUNTRIES WITH THE MOST FENCE STUDIES

Country	Percent of total studies
USA	20.9%
NA	11.5%
Australia	10.6%
South Africa	8.8%
China	6.7%
Botswana	4.0%
Kenya	3.4%
Canada	2.9%
New Zealand	2.9%
Spain	2.5%
United Kingdom	2.2%
Scotland	2.0%

Chapter 5. Concluding remarks

This dissertation has been ambitious in its scope, but its chapters cohere in their interest in improving our understanding of the links between human beliefs, behaviors, and their ecological consequences. I drew widely from analytical techniques developed in movement ecology, community ecology, human-wildlife conflict, social science, and even psychology to build case studies probing these links. While these chapters transgress traditional disciplinary boundaries, the research they contain makes a case for the importance of interdisciplinary thinking in the Anthropocene. And while the Anthropocene has ushered in many forms of environmental degradation to which this research responds, its effects have also degraded the need for distinguishing science that is primarily "theoretical" from science that is primarily "applied." When the human footprint touches even the most remote locales on the planet, theory and application can and should constantly remain in dialogue, and we might celebrate rather than avoid opportunities for their overlap.

This dissertation also draws influence from a body of literature questioning perceived divisions between humans and nature. Humans clearly have a special significance in an era named for our impacts, but often this distinction blinds us from our own active participation in the ecological relationships occurring around us. Chapter 2 highlights this tension with particular clarity: while the global impacts of human hunting distinguish us as a "super predator," the mechanics of that hunting remain more mysterious than those of many wild predators. The tools of ecology that have offered profound insights regarding wildlife have much to offer in understanding the ecological agency of humans, especially at fine scales. New technologies like GPS telemetry and camera traps have enormous untapped potential to unveil important findings not just about how humans impact the environment, but how they function and behave as a component of larger systems.

Chapter 3 takes up this theme of human-environmental reciprocity more directly. While the methods of wildlife ecology have growing room to apply to humans, ecologists would be limited if we did not also use the mature approaches of social science to help understand how humans perceive, respond, and act in their environments. However, disciplinary boundaries often enforce real partitions in sharing and understanding findings, as jargon, methods, and interpretations can be difficult to translate between fields. Chapter 3 shows that there is possibility and promise in linking these parallel approaches, and that doing so can provide complementary results. In fact, this chapter calls attention to serious consequences for inference when knowledge is too siloed, as our investigations using social methods revealed a systematic and as yet unreported bias within the increasingly popular ecological method of predation risk modelling. Future research along these lines can continue to break down boundaries between theory and application, between disciplines, and even between researcher and subject by recursively sharing and implementing findings with stakeholders and adapting accordingly. This two-way exchange of knowledge benefits the science of ecology, and it also builds trust and participation with managers, producers, and residents that is hard to establish any other way.

Fences are emblematic of many of the calls to action I have sounded above. They divide and link the landscape through their manifold effects, understanding these effects demands radical integration of multiple disciplines, and a robust "fence ecology" requires a seamless combination of theoretical and applied approaches to science. Like many of the drastic changes in the Anthropocene, fences seem to remain invisible until searching reveals profound global

changes. The antidote to their invisibility is narrating the dramatic stories of fences in the environment and depicting the secret snowballing of individual responses up to global changes.

Stories are vital to linking humans and ecology. Ecologists often lament our "physics envy," that we must allow for context, for application, and rarely discover eternal, universal truths through elegantly controlled experiments. However, there is a kinship between science and storytelling, and, noticing this, we might also recognize that context-dependence is a strength, giving life and detail to our stories, and making them tangible and available to diverse audiences. Listening to the stories around us might also remind us that many human-wildlife conflicts are, at root, human-human conflicts. Stories are vital access points to these conflicts and to understanding the people and behaviors at work within them. Stories thus give ecologists power to discover, to engage, and to learn. And, lastly, vitally, a fluency in the stories of the people we work with helps ensure we recognize their personhood. Stories give us both a tool and a motivation to develop approaches that mitigate the effects of the Anthropocene for the natural world and also make it a more just and liveable era for people. I hope the research included here helps make a small step toward these goals.

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